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An Evaluation of Two Tags with Northern Pike (*Esox lucius*)

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KOSHINSKY, G. D. 1972. An evaluation of two tags with northern pike (*Esox lucius*). J. Fish. Res. Bd. Canada 29: 469–476.

In a 4-year study of northern pike (*Esox lucius*) at Lac la Ronge, Sask., barb-anchored spaghetti dart tags (when applied with special needles and disinfectant) were retained longer than monofilament-attached preopercular disc tags. Losses after 2 years were 13 and 92%, respectively. Tagging mortality tended to be higher among dart-tagged individuals, but was only 12% after 2 years. Condition tended to be depressed by both tags and, among females, more so by the preopercular discs. Growth increments tended to be smaller for disc-tagged than for dart-tagged individuals of the same sex. Disc-tagged pike also dispersed more widely and were more vulnerable to angling. It is suggested that a brightly colored tag attached to the head of a predatory species, such as pike, interferes with feeding, perhaps by startling prey; such interference would explain all of the comparative tagging effects observed.

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Au cours d'une étude effectuée au lac La Ronge, Saskatchewan, qui a duré quatre ans, les grands brochets (*Esox lucius*) ont gardé les marques-dards, type spaghetti, ancrées par un barbillon (inséré avec une aiguille spéciale et un désinfectant) plus longtemps que les disques préoperculaires attachés par un monofilament. Les pertes, après deux ans, ont été de 13 et 92% respectivement. La mortalité due au marquage eut tendance à être plus élevée chez les individus marqués au dard, mais n'était que de 12% après deux ans. Les deux marques ont affaibli la condition générale des poissons, mais le disque préoperculaire a eu, chez les femelles, un effet plus prononcé. La croissance a été plus faible chez les poissons marqués au disque que chez ceux de même sexe marqués au dard. De plus, les brochets portant un disque se sont dispersés davantage et ont été plus vulnérables à la pêche à la ligne. Nous croyons qu'une marque de couleur brillante fixée sur la tête d'un poisson prédateur comme le grand brochet nuit à l'alimentation, peut-être parce qu'elle effraye les proies; une telle interférence expliquerait toutes les différences observées avec ces deux marques.

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In a comprehensive investigation of the ecology and management of northern pike, *Esox lucius* Linnaeus, in Lac laRonge from 1966 to 1969 (Koshinsky MS 1972), considerable effortwas devoted to tagging as a basis for estimating the size of the population and the movement of individuals. The study required an individually distinguishable external tag that could be easily and rapidly applied under adverse weather and working conditions, caused minimal mortality, had good retention, did not increase vulnerability to exploitation, and would be readily discernible upon external examination of the fish. On this basis two tags were selected: an externally attached plastic disc of the Atkins type, and a barb-anchored spaghetti dart. This paper describes the two marking procedures, assesses mortality and loss coefficients, and explores the comparative effects of the two tags on condition, growth, movement, and vulnerability to angling.

Northern pike were obtained for tagging during spawning runs in Kinosao and Thomas creeks. Kinosao Creek enters English Bay on the west shore of the lake at 55°13′N, 105°18′W; Thomas Creek enters along the north shore at 55°17′N, 104°49′W. Pike captured were invariably mature, and usually of a size vulnerable to angling and gillnetting (Koshinsky MS 1972). Only 3% of those tagged were under 17 inches (43 cm) fork length. A total of 3984 tags were applied during these operations.

Marking Procedures and Materials

Fish for marking were taken in cotton poundnets during the spawning runs at Kinosao Creek in 1966 and 1967, and at Thomas Creek in 1967. Recaptures were obtained from 1967 through 1969. Tagging mortality and tag loss were studied exclusively at Kinosao Creek. Growth and post-spawning dispersal were examined at both locations. Dispersal data were obtained chiefly from the angling fishery in Lac la Ronge proper (Koshinsky MS 1969).

The spawning runs coincided with low water temperatures (usually 4–8 C), a favorable circumstance for the confinement and handling of fish. Pike were routinely sexed, measured to the nearest $\frac{1}{10}$ inch (2.5 mm), and examined for fin anomalies. Representative individuals were also weighed and sampled for scales. Three-man tagging teams proved the most convenient and efficient, with one man delivering and holding the fish, another tagging and taking scale samples and observations, and the third loading tag applicators and keeping records. Tagging was also done by two-member teams with the aid of a tape recorder, anesthetization of the fish using M.S. 222, or both. All the larger individuals were anesthetized, concentrations of 50–100 ppm being satisfactory at the temperatures prevailing. Fish were released upstream immediately after handling. The poundnet leads acted as a holding enclosure for post-tagging observation.

Dart Tags

The dart tag used was the Floy[1] FT-6A (Lawler and Smith 1963) with a 60-mm length of flexible polyvinyl-chloride tubing attached to a 16-mm nylon shaft equipped with 3-mm double barbs. These tags were yellow, numbered serially, and bore instructions for return. They were inserted on the left side, 1.5–2 cm below the dorsal fin and approximately two-thirds of the way back from the fin origin. In 1966, dart tags were applied with pointed forceps. The same instrument was used to remove three or four scales from the tagging site and to make a preliminary cutaneous perforation. The tip of the tag was delivered to a depth of about 1.5 cm, and the tag was twisted a quarter turn to anchor the barbs against the dorsal pterygiophores.

High dart-tag loss in the first year prompted the use of tagging needles for subsequent applications. Needles were constructed from 3-mm (outside diameter) stainless steel tubing soldered into an adapter made from Weatherhead 3224×2 and 48×2 brass fittings. Tubing (4 cm) was fitted to protrude from the adapter, which was forced into a 10-cm length of $\frac{1}{2}$-inch (1.3-cm) copper pipe to serve as a handle. The design permitted reversal of the needle shaft into the handle for convenient storage and transport. A similar apparatus has been described by Bidgood (MS 1968).

Needles were loaded by inserting the tag, butt end first, into the needle shaft as far as it would go (i.e. with one barb coming to rest inside the shaft). After removing a few scales from the area as described above, tags were applied at a shallow angle from the rear to depths of 2–4 cm, depending on the size of the fish. A quarter-turn rotation anchored the protruding barb, and the tagging needle was carefully withdrawn. A bead on the needle handle positioned in the same plane as the protruding barb facilitated proper delivery and anchoring of the tag. Needle tips were kept sharp and at a 20° bevel to facilitate penetration. Loaded needles were immersed vertically to the lengths of the tags in 0.5% lysol prior to tag application. A $\frac{1}{2}$-gal plastic bottle with the top cut down, and with a heavy rubber false bottom and a 10-holed wooden lid, proved ideal for this purpose. Ten disinfected tags could be delivered serially from this container with a single stop for re-loading.

Times for application of dart tags by a three-man team averaged 28 sec per application, with little deviation. This included removing the fish from the retaining tank, recording length, sex, and external condition, taking a scale sample, applying the tag, and preparing and loading tagging needles.

Disc Tags

The disc tags were of yellow laminated oval plastic, measuring 14×8.5×0.8 mm, with a 1-mm hole centered at one end. They were obtained by size description, numbered serially, and bore instructions for return. They

[1]Trade names referred to in this publication do not imply endorsement of commercial products.

were applied after the manner of Crossman (1956), as elaborated by Dr Crossman through personal communication. About 12 cm of 8-lb test (280μ diameter) monofilament nylon fishing line was tied to each tag with a fisherman's knot, and the free line at the knot was clipped to about 5 mm. The line was delivered under the left preopercular bone with a curved stainless surgical needle and needle holder, then carefully knotted with four consecutive half hitches. For most fish, round, half-circle, spring eye needles (Herco Brand French Intestinal No. 355, size 2) were completely satisfactory. More robust half-circle needles, such as Martin's Uterine No. 565, size 4 with cutting edge, were more effective for tagging the largest individuals. Round needles tended more to accumulate scales on their tips than did cutting-edge needles. However, the latter made a wider incision, particularly if the fish struggled during the application.

Times for application of disc tags averaged slightly over 1 min per tag, including tag preparation and the regular handling and sampling operations. This was more than double the time required for application of dart tags. The basic cost of the disc tags, however, was only about one-third as great.

Finclipping

Parts of specific paired fins were clipped in conjunction with tagging at Kinosao Creek to establish accessory marks for determining tag loss and tagging mortality. Fins were sheared one-half to two-thirds across on the trailing edge, and about one-third of the way out from the base. This portion of the fin was then torn away along the membrane between rays. Clipped fins were thereby left at least partially serviceable, presumably lessening adverse effects. Another advantage of partial clips is that they appear to be without natural analogs. Completely missing fins, on the other hand, had a 0.3% incidence in the population (Koshinsky MS 1972).

Regeneration, which usually occurred, was accompanied by a distinctive thickening and bending of rays along the excision line. This virtually eliminated difficulties in the recognition of finclips over the 2-year period of observations. However, these clips proved unreliable as marks among the smaller pike beyond this time interval.

Tag Loss

Tag loss rates were determined at Kinosao Creek for dart and disc tags placed in 1966, and for dart tags placed in 1967.Separate loss rates for dart tags were calculated for the two years because of the radical change in tagging procedure. Loss rates (Table 1) were estimated as percentages of finclipped recaptures lacking tags.

Dart-tag loss was high (37.7% after 1 year, 48.7% after 2 years)among fish tagged in 1966. This is in large measure attributabe to the unsophisticated tagging procedure used the first year. Use of refinements in 1967 markedly reduced this rate of loss to 9.8 and 13.0% after 1 and 2 years, respectively.

TABLE 1. Estimates of 1- and 2-year tag losses and tagging mortalities for disc tags, and for dart tags applied by two procedures[a] among northern pike at Kinosao Creek.

	1966	1967	1968	1969
Numbers of releases				
Dart tags, right pectoral clipped	555	–	–	–
Dart tags, right pelvic clipped	–	663	–	–
Disc tags, left pectoral clipped	515	–	–	–
No tag, left pelvic clipped	512	–	–	–
Numbers of recaptures				
Dart tags from 1966	–	144	60	–
Right pectoral clip only	–	87	57	–
Dart tags from 1967	–	–	185	94
Right pelvic clip only	–	–	20	14
Disc tags from 1966	–	161	10	–
Left pectoral clip only	–	46	112	–
Left pelvic clip	–	219	123	–
Tag losses (%)				
Dart tags, 1 year	–	37.7	9.8	–
2 year	–	–	48.7	13.0
Disc tags, 1 year	–	22.2	–	–
2 year	–	–	91.8	–
Tagging mortalities (%)				
Dart tags, 1 year	–	2.9	–	–
2 year	–	–	12.0	–
Disc tags, 1 year	–	5.9	–	–
2 year	–	–	1.6	–

[a]Dart tags applied with forceps in 1966; with tagging needles in 1967.

Disc-tag loss was moderate initially (22.2% after 1 year), but increased to 91.8% after 2 years. Examination of over 900 disc-tag recaptures at Lac la Ronge, some of them extant 3 years, disclosed no knot slippage or deterioration of tags or attaching line. Loss of these tags is attributed entirely to movement of the line through the preopercular bone, a phenomenon exhibited in varying degrees by the majority of disc-tag recaptures. Tag shedding was followed by reformation of the bone, so that there was often little superficial evidence of a tag's former presence. Loss of disc tags was most rapid among the smallest individuals (Fig. 1). Loss rates were similar for the two sexes at corresponding sizes.

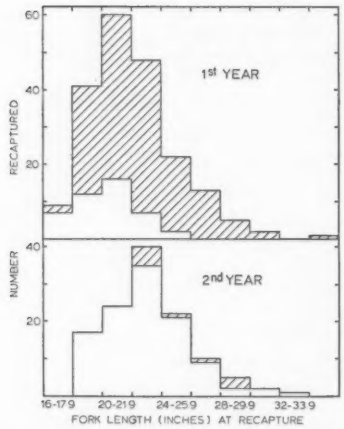

FIG. 1. Numbers of northern pike, according to size at recapture, which retained (cross-hatched bars) and lost (open bars) disc tags during the first and second years following tagging at Kinosao Creek in 1966.

Loss rates determined in this study did not differ appreciably from those reported for the same tags with other fish species. Armstrong and Blackett (1966) found an 11.3% dart-tag loss after 120 days among Dolly Varden (*Salvelinus malma*) larger than 150 mm (6 inches). However, after 494 days loss had increased to 27.7%. The tagging procedure was identical to that followed at Lac la Ronge in 1967, except that a single-barbed dart was employed and no mention was made of the use of disinfectant. Muir (1963) found preopercular disc-tag losses of 8.5, 30, and virtually 100% among muskellunge (*Esox masquinongy*) after 1, 2, and 3 years.

Tagging Effects

On Mortality

Tagging mortalities were estimated by comparing recapture ratios for tagged fish with those for fish that were finclipped but not tagged. As concluded by many investigators (e.g. Churchill 1963; Coble 1967), though not others (e.g. Ricker 1949), finclipping was assumed to make no significant contribution to mortality.

The 1- and 2-year mortalities were estimated as 2.9 and 12.0% for dart tags, and as 5.9 and 1.6% for disc tags (Table 1). There was no apparent reason for the observed decrease in disc-tagging mortality, which, in any event, was of low magnitude.

The literature contains some references to tagging mortality resulting from dart tags with other species, but apparently none for disc tags as employed here. Armstrong and Blackett (1966) deduced a one-season dart-tagging mortality of less than 6% for Dolly Varden larger than 150 mm (6 inches) fork length. Smaller char suffered higher post-tagging mortality as a result of selective predation induced by the yellow tag. McDonald (MS 1969) observed a 24-hr dart-tagging mortality of 12.4% for northern pike; however his fish were taken by gillnetting and angling, which may have impaired their condition. Kennedy (1970) found virtually 100% mortality within 1 year among dart-tagged sablefish (*Anoplopoma fimbria*) held captive in tanks or retaining nets.

On Condition

Condition coefficients for tagged and untagged northern pike in the 1968 Kinosao Creek spawning run were calculated according to the summer length–weight relation (Koshinsky MS 1972), i.e.:

$$\text{condition coefficient} = (\text{weight in ounces} \times 10^3)/(\text{fork length in inches})^{3.11}.$$

Since the gonads comprise a significant fraction of body weight among spawning females, determinations (Table 2) were confined to individuals which appeared completely gravid.

A slight but consistently detrimental effect of tagging on condition was indicated, and differences between tagged and untagged fish were statistically significant ($P < 0.05$) for males. These appeared to be affected identically by the two tags, whereas disc-tagged females tended to be lighter at specific lengths than their dart-tagged counterparts. There was more variability in condition among females of all categories, perhaps reflecting differences in gonad proportions or, despite sampling precautions, in gonad evacuation.

TABLE 2. Condition coefficients for tagged and untagged northern pike according to sex, Kinosao Creek, 1968.

	Untagged	Dart-tagged	Disc-tagged
		Males	
No. fish	65	69	33
Coefficient	3.05±0.029[a]	2.95±0.024[b]	2.95±0.033[b]
		Females	
No. fish	70	78	28
Coefficient	3.17±0.033	3.13±0.030	3.08±0.042

[a]One standard error of mean.

[b]Difference from the value for untagged significant at $P<0.05$ (t = 2.54 and 2.01).

On Growth

The relative effects of the two tags on growth were examined by comparing 1-year post-tagging increments according to sex and length at tagging. Greater increments tended to be achieved by dart-tagged than by disc-tagged northern pike of all categories at Kinosao Creek (Fig. 2). However, the differences were significant ($P < 0.05$) only among males less than 20 inches long at tagging. A similar evaluation for the Thomas Creek spawners failed to disclose any significant differences in growth according to tag type.

An indication of the absolute effect of tagging on growth was sought by superimposing the slopes of the 1-year post-tagging increments over the corresponding portions of smoothed growth curves calculated for unmarked northern pike (Koshinsky MS 1972). Separate plots were employed for the two locations and the two sexes because of inherent differences in growth. The greatest effect of tagging was evident among the smallest fish; the effect was negligible among those larger than 26 inches at tagging (Fig. 3).

On Dispersal

Posts-pawning dispersal of tagged pike was analyzed from summer tag returns, primarily from the angling fishery. There was no apparent difference in dispersal between the sexes, nor any notable tendency for pike to be taken at progressively greater distances from the tagging site in successive seasons (Koshinsky MS 1972). This permitted pooling of the data in these respects for an examination of the influence of tag type on movement.

Wider summer dispersal with increasing size was characteristic of northern pike bearing either tag (Fig. 4). This was coupled with a consistent tendency for disc-tagged individuals to range farther than their

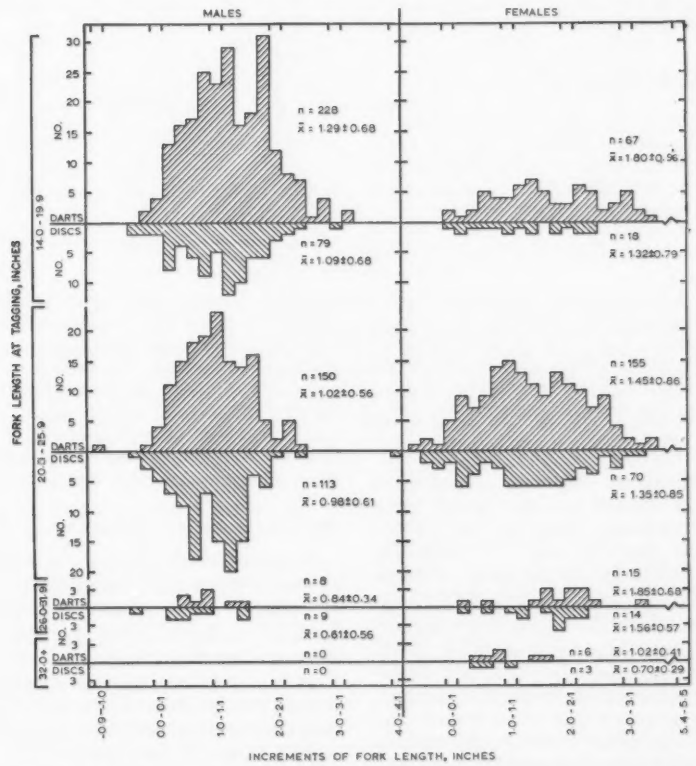

FIG. 2. One-year increments in fork length according to tag type, sex, and length at tagging for northern pike tagged and recaptured at Kinosao Creek, 1966–67 and 1967–68 (pooled). Also given are sample sizes, means, and standard deviations of means of increments in each category.

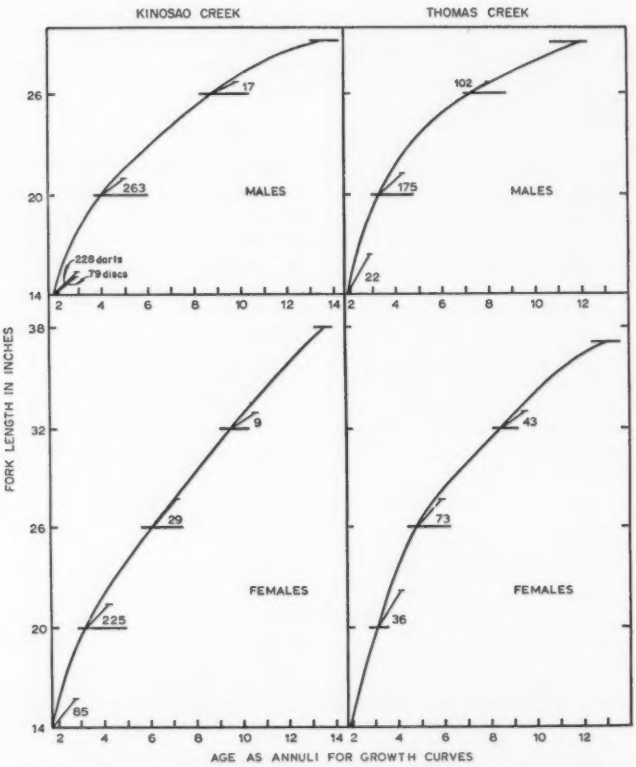

FIG. 3. Comparative growth of tagged and untagged northern pike of each sex from two Lac la Ronge tributaries. The smoothed, continuous curves are for unmarked pike (Koshinsky MS 1972); the short ascending lines denote mean 1-year growth increments for tagged fish (irrespective of age) within the length ranges indicated. Numerals near the increment lines denote numbers of fish; data for the two tags were pooled except in the one instance where growth was significantly different.

dart-tagged counterparts. The observed dispersal patterns were significantly different ($P < 0.05$) for the two tags for all but the smallest pike, i.e. those under 20 inches fork length at tagging. Clancy (1963) demonstrated that disc tags inserted through the musculature effected a permanent drop of about 50% in swimming endurance among fingerling steelhead trout (*Salmo gairdneri*). Performance was poorer among loosely tagged than among tightly tagged fish, indicating that hydraulic drag was the main determining factor. Spaghetti darts, properly applied, presumably offer little resistance to water flow (Yamashita and Waldron 1958). However, the presence of any foreign object in the musculature might reasonably be expected to reduce the ability of a fish to swim. It could be concluded that dart tags, as used in the present study, had a greater adverse effect on dispersal than did disc tags. However, the alternative, that the preopercular disc tags may have stimulated movement of pike, merits consideration.

On Vulnerability to Angling

Disproportionately more disc-tagged than dart-tagged northern pike invariably occurred in creels, athough the recovery ratios were significantly different ($P < 0.05$) in only one instance (Table 3). That this cannot be attributed to better disc-tag retention, lower disc-tagging mortality, or both, has already been indicated. Either dart-tagging decreased the vulnerability of northern pike to angling, or disc-tagging increased this vulnerability.

Discussion and Conclusions

The trends to greater dispersal and vulnerability to angling observed among disc-tagged than among

dart-tagged northern pike in this study may have been due to a greater impairment of mobility among the latter group. However, the weak but consistent tendency for disc-tagged pike to suffer greater reduction in growth and condition indicates that it was actually this category that was the more seriously affected. Kelly and Barker (1963) noted greatly reduced growth of redfish (*Sebastes marinus*) marked with disc tags placed on the operculum, and postulated that these tags had a "signal" effect, startling prey when the fish attempted to feed. Lawler and Smith (1963) obtained a significantly lower return opaque yellow tags than of clear transparent tags among yellow perch (*Perca flavescens*), and concluded that the colored tags subjected the perch to increased predation. Armstrong and Blackett (1966) observed a similar effect among small Dolly Varden. The potential of tagging to significantly alter the feeding relations among fishes is thus well established. Maximal disruption of feeding for a predatory species such as pike would presumably be achieved by a brightly colored tag attached anteriad. The preopercular discs used in the present study had these characteristics. It is accordingly indicated that the differential tagging effects that were observed might be linked to, and would certainly be consistent with, a diminished feeding ability among disc-tagged individuals.

The lesser adverse effects of dart tags, along with their better retention and greater speed and convenience of application, favor them over the Atkins type, at least as exemplified by the specific models and attachments used among northern pike in this study. The mechanism of disc-tag loss suggests that improved retention might be achieved by the use of a stouter attachment line, or by one that is flat in cross-section. The advantages of the dart tags are tempered by their considerably greater cost.

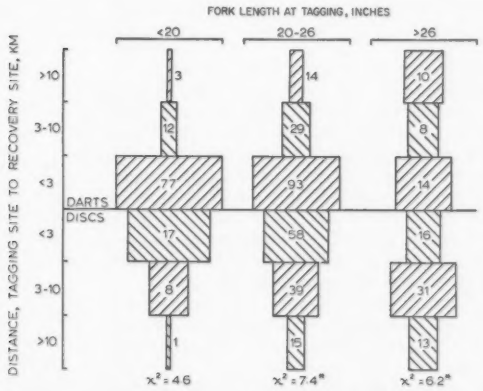

FIG. 4. Numbers of northern pike of different lengths at tagging that were recovered at various distances from the tagging sites. Data pooled on the basis of sex, tagging sites (Kinosao and Thomas creeks), and time extant (1–3 years). Asterisks indicate significant differences ($P < 0.05$) in dispersal between the two tags.

TABLE 3. Rates of recovery by angling in year of tagging of two tags applied to northern pike at two sites in Lac la Ronge, 1966 and 1967.

Year	Application site	Tag	No. tagged	Recovered (%)
1966	Kinosao Creek	Dart	555	4.14[a]
		Disc	515	7.96[a]
1967	Kinosao Creek	Dart	1480	6.82
		Disc	432	8.10
1967	Thomas Creek	Dart	301	3.99
		Disc	701	5.71

[a]Difference significant at $P < 0.05$ ($X^2 = 6.26$).

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Population Biology of Alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949-70[1]

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BROWN, E. H., JR. 1972. Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949–70. J. Fish. Res. Bd. Canada 29: 477–500.

Alewives were unknown in Lake Michigan before 1949, but became extremely abundant in the 1960s and soon exceeded the carrying capacity of the lake. In 1967 they were decimated by a lakewide mass mortality, and have since been less abundant as "adults" (≥120 mm long), although numerous young were produced in 1967–70 and the adult population appeared to be gradually increasing. Alewives were studied intensively during 1962–70 on the basis of collections made primarily with bottom trawls. Principal considerations in the population study include effects of seasonal changes in distribution on length composition of young and adults, sex and maturity in relation to size and age at recruitment into adult stocks, and changes in age, growth, condition, and population structure that accompanied the drastic changes in abundance.

A substantial increase in the age of adults in the bottom stocks and on the spawning grounds was among the important population changes after the 1967 die-off. Growth of older adults also increased appreciably immediately after the die-off, and a sharp increase in average weight (16–26%) over a standard range of lengths was maintained in 1968–70. Selective depletion of zooplankton by alewives was evidence that overabundance decreased the food supply, depressed growth, and caused the poor condition that made alewives vulnerable to excessive mortality in 1967. Although poor condition in fall undoubtedly increased winter and spring mortality in the mid-1960s, alewives apparently were stressed by below-average temperature in the winter of 1969–70, and experienced a light die-off through May 1970 despite their good condition and relatively low population density the preceding fall.

The population upsurge that preceded the 1967 die-off was reflected by a fivefold increase of adults in the fall index catch (in trawls) from 1962 to 1965 and 1966. The index catch then dropped 70% in fall 1967. Mortality among the 1960–64 year-classes, as represented by annual losses from age III to age IV in the index catch during 1964–68, ranged from 40% in 1965 to 89% in 1967, and averaged 68%. Assessment of mortality from the index catches was difficult because the age of alewives at full recruitment into bottom stocks increased from III in the mid-1960s to IV or older in 1968–70, when alewives remained longer at midlevels, possibly because of a delay in sexual maturity. Annual mortality after the fifth year of life, on the basis of average percentage age composition of the trawl catches in 1964–70, was tentatively estimated as 79–80%. The number of alewives recruited to the adult population from the 1962–67 year-classes over several ages in the fall index catch was inversely related to the abundance of their parents in the fall immediately preceding the year in which each year-class was spawned.

Annual commercial production in the 1960s (peak in 1967, 42 million lb) may not have exceeded 7.7–18.6% of the bottom stocks, on the basis of the estimated weights of alewives available to trawls in the spring of 1964 and 1969. Yield per recruitment to the commercial fishery was low because of slow growth and high natural mortality.

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Il n'y avait pas de gaspareaux dans le lac Michigan avant 1949, mais ils sont devenus extrêmement abondants au cours des années 60 et ont rapidement dépassé le potentiel biotique du lac. En 1967, ils furent décimés par tout le lac par une mortalité catastrophique et, depuis ce temps, les "adultes" (≥ 120 mm de longueur) sont moins nombreux, bien qu'un nombre considérable de jeunes soient apparus de 1967 à 70 et que la population adulte semble augmenter graduellement. Le gaspareau a fait l'objet d'études intensives de 1962 à 1970, basées sur

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des échantillons prélevés surtout au chalut de fond. L'étude a porté principalement sur l'influence des changements saisonniers de répartition sur les fréquences de longueur des jeunes et des adultes; la taille et l'âge au moment de l'entrée dans les stocks adultes; et les variations de l'âge, de la croissance, de l'état d'embonpoint et de la structure des populations qui ont accompagné les violentes fluctuations d'abondance.

Une des modifications importantes qu'ont subi les populations à la suite de la mortalité de 1967 a été un accroissement substantiel de l'âge des adultes des populations benthiques et de celui des reproducteurs sur les frayères. La croissance des plus vieux adultes a augmenté sensiblement aussitôt après la mortalité. Il y eut également brusque accroissement du poids moyen (16–26%) sur une gamme de longueurs bien définie, et qui s'est poursuivi de 1968 à 1970. L'appauvrissement différentiel du zooplancton, dont les gaspareaux furent responsables, a prouvé que leur surabondance a abaissé les réserves alimentaires, ralenti la croissance et causé une maigreur qui les a rendus vulnérables à la mortalité catastrophique de 1967. Quoiqu'un pauvre état d'embonpoint à l'automne ait favorisé une mortalité accrue en hiver et au printemps vers le milieu des années 60, les gaspareaux ont eu à subir la contrainte de températures au dessous de la moyenne durant l'hiver 1969–70. Ceci a entraîné une légère mortalité jusqu'en mai 1970 en dépit d'un bon état d'embonpoint et d'une densité de population relativement faible à l'automne précédent.

L'explosion des populations qui a précédé la mortalité de 1967 a été marquée par une augmentation de cinq fois la prise-indice automnale des adultes dans le chalut de 1962 à 1965 et 1966. A l'automne 1967, la prise-indice diminuait de 70%. La mortalité des classes d'âge de 1960 à 1964, soit la décroissance annuelle en nombres entre les âges III et IV dans les prises-indice de 1964 à 1968, a varié de 40% en 1965 à 80% en 1967. Le calcul de la mortalité à partir des prises-indice a été compliqué par le fait que l'âge des gaspareaux au moment de leur pleine entrée dans les populations benthiques a augmenté de III au milieu des années 60 à IV et plus en 1968–70. Les gaspareaux avaient alors séjourné plus longtemps à des profondeurs intermédiaires, possiblement par suite d'une maturité sexuelle tardive. La mortalité annuelle après la 5ième année, calculée à partir du pourcentage moyen de fréquence d'âges dans les prises du chalut de 1964 à 1970, a été estimée provisoirement à 79–80%. Le nombre de recrues rejoignant la population adulte à même les classes d'âge de 1962–67 et englobant plusieurs âges dans la prise-indice automnale était en fonction inverse de l'abondance des parents à l'automne précédant immédiatement l'année de naissance de chaque classe d'âge.

Basée sur un estimé du poids des gaspareaux accessibles au chalut aux printemps 1964 et 1969, la production commerciale annuelle des années 60 (sommet en 1967: 42 millions de livres) peut ne pas avoir excédé de 7.7 à 18.6% du stock benthique. Le rendement par recrue entrant dans la pêche commerciale était faible, par suite d'une croissance lente et d'un taux de mortalité naturelle élevé.

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ALEWIVES have had a powerful impact on the ecology of Lake Michigan since they were discovered near South Manitou Island (Fig. 1) in 1949 (Miller 1957). Possible signs of population pressure on other species, as alewives became increasingly abundant during 1949–66, include drastic declines of emerald shiners (*Notropis atherinoides*), lake herring (*Coregonus artedii*), and kiyis (*C. kiyi*) and population instability of bloaters (*C. hoyi*), the only deepwater cisco still abundant in Lake Michigan (Smith 1970; Brown 1970).

Destruction of predators by sea lampreys (*Petromyzon marinus*) has been suggested as the ecological change that enabled alewives to become the dominant species in Lake Michigan (Smith 1970). After lake trout (*Salvelinus namaycush*) were near extinction (Eschmeyer 1957) and burbot (*Lota lota*) had become extremely scarce, spawning migrations of alewives were established in the 1950s in northern Lake Michigan and Green Bay (Joeris and Karvelis MS 1962). The invasion then progressed rapidly into southern Lake Michigan, where heavy die-offs and blocked industrial and municipal water intakes were costly nuisances in the mid-1960s. An unprecedentedly high abundance of adult alewives in southern Lake Michigan in 1965 and 1966 was followed by a massive die-off along almost the entire circumference of the lake in June and July 1967 (Brown 1968). The tourist industry lost millions of dollars because of fouled beaches, and the alewife problem received national attention (Time July 7, 1967).

Industrial use of alewives for pet food and fish meal developed as the stocks expanded. Landings, mainly from trawls and poundnets, were nearly 42 million lb (19 million kg) in 1967 (Table 1). At the peak of the fishery, eight trawlers operated from Wisconsin ports on Lake Michigan and in Green Bay and three from Saugatuck, Mich., in southeastern Lake Michigan. The poundnet fishery

was largely in Green Bay, although poundnets were also fished at Milwaukee.

The invasion and rapid establishment of alewives in Lake Michigan provided unusual opportunities to study population changes in this species that were unfolding on a huge scale. The present study is part of a continuing effort to monitor the population changes and determine the role of alewives in the changing ecology of the lake.

FIG. 1. Lake Michigan, showing localities mentioned in the text. Scale is in statute miles.

TABLE 1. Commercial landings (*thousands of pounds*) of alewives in different gears, Lake Michigan, 1956–70.

Year	Gear			
	Trawl	Poundnet	Other[a]	Total
1956	–	–[b]	–[b]	–[b]
1957	–	185	36	220
1958	55	1241	61	1356
1959	59	1057	149	1264
1960	526	1787	57	2370
1961	2048	1121	29	3199
1962	2309	2381	53	4742
1963	3493	1897	6	5396
1964	7760	3969	14	11,743
1965	11,420	2556	32	14,007
1966	18,548	10,424	30	29,002
1967	19,535	22,338	23	41,895
1968	13,085	13,791	318	27,194
1969	14,226	14,839	183	29,248
1970	15,411	17,997	52	33,461

[a]Gillnets, fykenets, and trapnets.
[b]Less than 500 lb.

Sampling Methods

Alewives were sampled on the bottom and in midwater in Lake Michigan and in tributary rivers. Experimental trawling on the bottom at depths of 3–50 fathoms (5.5–91.5 m) off Saugatuck (Fig. 1) each spring and fall in 1962–70 and in the summers of 1965–66 was the main source of material for this study. The semiballoon nets had 39-ft (11.9-m) headropes, 51-ft (15.5-m) footropes, and ½-inch (1.3-cm) mesh (stretched measure) codends. Supporting information about alewives in midwater was obtained with gillnets fished obliquely at Saugatuck in 1962 and with a British Columbia herring trawl fished off Saugatuck and Grand Haven, Mich., and between Saugatuck and Racine, Wis., in 1965. Records from fishery surveys in 1954–55 and 1960–61 with trawls and gillnets at various locations in Lake Michigan were also used. Aggregations of spawning alewives were dipnetted at night near shore in the Kalamazoo River at Saugatuck (1965–66; 1968–70) and the St. Joseph River at Benton Harbor (1968–70). Alewives were also sampled by hand from water intake screens of the Chicago Central District Filtration Plant in April–June 1966.

Relative abundance was assessed by systematic trawling with the standard nets, mainly from the R/V *Cisco* in late October or November (1962–70) when alewives were near the bottom at all depths. Assessment was more difficult in spring because alewives migrated rapidly from deep wintering areas toward shallow water, and progress of the migration varied from year to year. In summer many were in midwater or spawning in the rivers. The standard 12-tow trawl transect included single tows along the contour at depths of 3, 5, 7, 10, 12, 15, and 17 fathoms (5.5, 9.1, 12.8, 18.3, 21.9, 27.4, and 31.1 m), and at 5-fathom (9.1-m) intervals from 20 to 40 fathoms (36.6 to 73.2 m). Engine speed was the same for all tows and vessel speed was about 2.6 knots. Tows usually lasted 10 min, but were shorter at 3 fathoms and occasionally at other depths where the bottom was rough. Catches in these shorter tows were adjusted to 10 min. The fishing was limited to a single transect off Saugatuck in 1962–66, but was extended in 1967–70 to two transects (run on separate days) off each of four ports: Saugatuck, Ludington, and Benton Harbor, Mich., and Waukegan, Ill. (Fig. 1). Both the R/V *Kaho* and the *Cisco* were used during this extended coverage. The 12 tows of each transect were completed on the same day in all years except 1962 and 1963. Unreplicated tows at 45 (82.3 m) and 50 (91.5 m) fathoms off Saugatuck were not used in abundance estimates, but provided length frequencies and sex ratios.

Indices of abundance for alewives in fall were also computed from statistics of the commercial trawl fishery in Michigan and Wisconsin waters of southern Lake Michigan. Catch–effort statistics were mailed by fisher-

men to the state conservation agencies and later were summarized at the Great Lakes Fishery Laboratory.

Alewives caught in the experimental trawls were sorted by total length into two groups: (1) young-of-the-year (fall) or yearlings (spring), and (2) fish with two or more seasons of completed growth, termed adults in this study. On the basis of length frequencies, the division between the two groups consistently fell near 120 mm (Table 2), which is the length used here as the lower limit for the adults; this group comprised mostly mature fish, but also some fish that were sexually immature. Alewives in each group were counted, weighed in the aggregate, and subsampled randomly for total lengths; each of the adult alewives in the subsamples (or in parts of the larger subsamples) was weighed, sexed, and scale-sampled.

Scales for the main age and growth analyses were sampled from trawl catches in April and late October or November at Saugatuck. Alewives from one to three trawling depths were represented in 1964–66 and from nearly all depths in 1967–70. Scales from alewives spawning in the Kalamazoo River in June–July 1965 and 1968–70 were pooled with the trawl samples for growth calculations. Age-groups are designated by Roman numerals corresponding to the number of annuli, and all alewives were considered to have passed into the next higher age-group on January 1.

Growth histories were calculated from the relation

$$L = S[(L_c - 27.6)/S_c] + 27.6$$

where L_c and S_c are, respectively, the length of fish and anterior scale radius at capture, and L is the calculated length of fish for a scale radius S at a previous annulus. The constant 27.6 is the intercept of the body–scale regression $L_c = 27.6 + 1.37\ S_c$ fitted by least squares to the mean radii of 604 key-area scales grouped in 5-mm intervals of fish length from 50 to 250 mm. The key scales were located 4–5 scale rows below the insertion of the dorsal fin near the area used by Havey (1961) for Atlantic Ocean alewives. Growth fields of the magnified scale image (42×) were measured from the focus, which appears as the center of concentric bands of varying optical density. The focus or true scale origin is immediately posterior to the principal transverse groove, which some workers have substituted for the origin (Rothschild 1963). In length calculations, annuli were credited at the edges of scales sampled between late October and the start of new growth the following summer.

Total weight of alewives available to bottom trawls over about 63% of the surface area of Lake Michigan and Green Bay was estimated from the catch per unit area by the *Kaho*, April 28–May 22, 1964 (Reigle 1969a, b, c). The *Kaho* made 131 30-min tows with a commercial trawl that had a 52-ft (15.9-m) headrope and 1-inch (2.5-cm) mesh codend at depths of 5–80 fathoms (9.1–145 m) at the following localities: Benton Harbor, White Lake, Ludington, Frankfort, Traverse City, and Manistique, Mich.; several areas in Green Bay; Sturgeon Bay, Manitowoc, and Port Washington, Wis.; and Waukegan, Ill. A similar estimate was obtained April 30–May 30, 1969, for about 51% of the surface area, on the basis of 206 10-min tows by the *Kaho* and *Cisco* with the standard trawl (39-ft semiballoon) at 3–50 fathoms (5.5–91.5 m) at the same localities (except White Lake and Traverse City) and at Saugatuck and South Haven, Mich. (Fig. 1).

The estimates of available alewives were summations of the weight per acre trawled, times total acres in sections of the lake represented by different localities and depths. Average catch rates in the various sections were expressed as geometric means because sample variation was large. An interval of one standard error (asymmetrical) was calculated for the part of each estimate obtained from sections with two or more trawl tows; however, single tows were included in computations of the total weight of alewives. The 1969 estimate of available alewives was expressed in terms of the 52-ft commercial trawl, by using the following relation calculated from 18 pairs of tows with the 52- and 39-ft trawls fished side by side from the *Kaho* and *Cisco*, respectively, at Saugatuck, October 1970 and April 1971:

$$\text{Log } y = 0.5209 + 0.8873 \text{ Log } x$$

where y is kilograms of alewives in a 10-min tow with the 52-ft trawl, and x is kilograms in a paired tow with the 39-ft trawl.

Various theoretical yields per recruitment of alewives to the trawl fishery in Lake Michigan were calculated by using an exponential model after Ricker (1958). Instantaneous fishing mortality (F) was distributed seasonally according to the percentage monthly distribution of commercial production in 1964–66 (described later). Natural mortality (M) was distributed hypothetically over the year, roughly on the basis of mortalities observed in the field and reported in the literature (Graham 1956 and Brown 1968). To allow for seasonal differences in mortality and growth, the period from November through October was subdivided as follows: November–December, F = 17%, M = 6%; January–March, F = 5%, M = 9%; April–June, F = 48%, M = 55%; July–August, F = 9%, M = 24%; and September–October, F = 21%, M = 6%. It was assumed for the model that alewives made 75% of their annual growth in July–August and 25% in September–October.

Length Composition

The length distribution of alewives sampled near the bottom changes considerably with seasonal changes in an extremely wide spatial distribution. Alewives winter in the deeper, warmer areas of the lake, move rapidly inshore in April and May, and spawn in the tributaries from late May to early August. Their return to deep water progresses slowly during late summer and fall. In the course of a year, alewives at various life stages occupy all water strata over bottom locations extending from inshore to midlake.

TABLE 2. Length–frequency distribution of alewives caught in experimental trawls at 3–50 fathoms off Saugatuck, Mich., spring and fall 1962–70.

Total length (mm)[a]	1962		1963		1964		1965		1966		1967		1968		1969		1970		Total	
	May	Nov.	May	Nov.	Apr.	Nov.	Apr.	Nov.	Apr.	Nov.	Apr.	Nov.	Apr. May	Nov.	Apr.	Oct.	Apr.	Oct.	Apr. May	Oct. Nov.
30–39	–	1	–	7	–	89	–	49	–	18	–	73	–	172	–	422	–	194	–	1025
40–49	–	42	–	211	–	1963	–	2198	–	480	–	1150	–	3073	–	2071	–	2921	–	14,109
50–59	–	86	–	571	–	4102	–	4736	–	815	–	693	–	4081	–	4732	2	8970	2	28,786
60–69	–	12	1	190	–	3415	2	1572	3	190	8	186	46	1898	98	6577	33	5202	191	19,242
70–79	9	9	16	96	1	3929	15	514	9	107	14	144	523	5941	378	5997	97	1729	1062	18,466
80–89	25	23	76	79	3	1833	10	141	11	86	21	106	1930	9877	537	7791	38	2008	2651	21,944
90–99	175	10	117	60	25	299	1	88	9	83	5	80	1878	2185	517	2156	19	1087	2746	6048
100–109	103	6	101	16	2	8	4	8	2	79	1	38	209	485	221	1034	8	106	651	1780
110–119	8	–	59	8	26	25	–	18	17	63	3	2	90	241	61	352	9	67	273	776
120–129	16	2	139	4	1	54	4	70	44	29	4	6	20	7	61	33	9	115	298	320
130–139	119	23	134	43	106	168	30	96	25	200	43	25	101	13	162	164	28	208	748	940
140–149	207	15	93	72	1150	141	87	197	279	501	90	68	167	47	214	165	37	72	2324	1278
150–159	226	51	66	146	2348	361	387	884	989	1240	407	289	559	67	362	118	117	93	5461	3249
160–169	315	92	166	229	3160	407	545	1648	1596	1739	869	897	1423	217	778	281	609	212	9461	5722
170–179	316	117	190	226	2708	371	367	1461	1159	1141	800	911	1278	305	825	541	1341	497	8984	5570
180–189	275	157	140	143	1396	258	157	714	425	415	430	450	678	232	519	524	1166	435	5186	3328
190–199	223	123	86	86	390	92	61	232	122	117	84	135	204	102	146	316	546	372	1862	1575
200–209	139	44	29	21	143	36	19	43	48	1	14	21	40	27	32	95	138	98	602	386
210–219	15	20	11	4	16	8	5	13	–	9	23	2	9	5	2	22	30	23	111	106
220–229	23	12	2	11	15	–	–	–	–	–	–	–	1	–	–	5	4	–	45	28
230–239	–	3	–	1	4	–	–	1	–	–	–	–	–	–	–	–	–	3	4	8
240–249	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Total young	320	189	370	1238	57	15,663	32	9324	51	1921	52	2472	4676	27,953	1812	31,132	206	22,284	7576	112,176
% measured	13	97	36	44	21	5	78	12	100	50	80	53	15	6	42	6	96	3	26	8
Avg length[b]	97	61	97	61	103	65	81	56	94	61	82	55	89	73	88	72	79	62	90	63
Total adults	1874	662	1056	986	11,437	1896	1662	5359	4687	5392	2764	2804	4480	1022	3101	2264	4025	2125	35,086	22,513
% measured	16	65	39	53	11	60	54	35	32	29	26	79	37	92	54	62	35	34	28	48
Avg length[b]	171	180	162	170	167	164	166	168	166	163	169	171	169	174	167	173	179	172	168	171

[a]Fish less than 120 mm long were considered as young-of-the-year (October–November) or yearlings (April–May).
[b]Average lengths for 1962–70 (columns at far right) are unweighted by years.

Young-of-the-year and Yearlings

During fall in 1962–70, young-of-the-year of below-average length (for fish of their year-class) concentrated near the bottom. Their dominant modal lengths in southeastern Lake Michigan were 50–59 mm in 1962–66 and 1970, 40–49 in 1967, and 80–90 in 1968–69 (Table 2), compared to an average length in the first year of 98 mm back-calculated from the scales of older fish. These smaller young were mostly in relatively warm water at various depths above the thermocline in fall, and extended their range to greater bottom depths in years when the thermocline had receded deeper in the lake (depth distribution shown later). Average lengths of young alewives in October and November increased consistently with an increase in distance from shore (Wells 1968), the small fish nearer shore presumably having hatched later than the larger fish taken deeper in the lake.

Modal lengths of yearlings sampled near the bottom in spring were usually greater than those of the young of the preceding fall, and average lengths were always greater in the spring (Table 2); in some springs modal lengths of yearlings corresponded closely with lengths back-calculated to the first annulus of adults. Size of the young in spring did not change in relation to the depth sampled. The small young on the bottom in fall apparently were in midwater in spring, although some may have died in winter. It is unlikely that they grew enough, if at all, in winter to account for their disappearance in the spring collections. Yearlings were scarce at depths of 3–50 fathoms in April but were more common in May and early June, when many moved inshore from wintering areas over deep water (Brown 1968). Those caught in trawls in relatively shallow water in spring and early summer presumably represented part of a predominantly pelagic population that was present only in midwater at greater depths. Later in summer, yearlings were almost entirely pelagic at the trawling locations and remained mostly at midlevels until their third summer.

Adults

That many young adults were at midlevels was demonstrated in May, July, and November 1962 by catches in gillnets fished from surface to bottom over bottom depths that averaged 13 and 26 fathoms (23.8 and 47.6 m). On May 23, before thermal stratification was well defined, 2-year-olds (modal lengths, 130–149 mm) were taken from all depth intervals at the 13-fathom location, but mainly toward the surface (Table 3). On July 6, when the lake was thermally stratified at the 26-fathom location, 2-year-olds were caught almost entirely in the surface layer, well above the thermocline. On November 6, when the lake was homothermous at the 26-fathom station except for a thin layer of cooler water at the bottom, yearlings were taken at all levels, but mostly above the range of bottom trawls.

Most adults in the trawl catches made near bottom (Table 2), at midwater, and during the spawning season were from a single modal group. Their highest length frequencies in the bottom collections were either at 160–169 or 170–179 mm in 17 of 18 sampling periods during 1962–70. Yearlings (fall) and 2-year-olds (spring) made up secondary modes between 120 and 149 mm in six collection periods, including, for example, October 1969 and 1970, when the 1968 and 1969 year-classes were strongly represented. In August 1965, the average lengths of 781 adults in the bottom catches (males, 159 mm; females, 165) were nearly the same as those of 347 caught in midwater (males, 160 mm; females, 167). The bottom population was concentrated at depths shallower than 20 fathoms (36.6 m), but in midwater adults ranged from inshore to midlake, at sampling depths of 3½–21 fathoms (6.4–38 m) over bottom depths of 15–87 fathoms (27–159 m). The length distribution of alewives spawning at night in the Kalamazoo and St. Joseph rivers in June and July was similar to that of adults in the spring and fall trawl collections: modal lengths of 2479 spawning alewives (mostly males) were between 160 and 179 mm in 1965–66 and 1968–70.

Alewives segregated by size over various bottom depths at different seasons. The annual spawning migration and seasonal thermal changes in the lake had marked effects on distribution. The largest adults led the shoreward migration in late winter and spring and the return to deeper water in summer and fall (Wells 1968). Average lengths tended to decrease with increasing depth in April and (more pronouncedly) increase with increasing depth in November (Table 4).

Sex and Maturity in Relation to Length

The sex composition of adults changed consistently in relation to increasing length of fish, as shown by the extensive trawl collections in 1965 and 1966 from southern Lake Michigan and the 1966 collections from the water intake screens at Chicago (Table 5). Numbers of males and females in the combined collections were nearly equal at 100–119 mm, the smallest fish for which sex was determined. The percentage females then declined to only 29–30% at 140–159 mm, before increasing steadily at all the greater lengths. Although some immature fish of both sexes are present in the modal group that here identifies adults ($\geq$120 mm), the

initial decline in percentage females at increasing lengths in that group reflects earlier sexual maturity for males. As they mature, males apparently adopt the habits and orientation of larger adults, and therefore become available to trawls at a smaller size than do females. The later maturing females are increasingly predominant at the greater lengths because they grow faster and live longer than the males.

The size differences between sexes at maturity were clearly exhibited by spawning alewives in the Kalamazoo and St. Joseph rivers (Table 6). Ripe males were represented at one or more 10-mm length intervals from 110 to 149 mm in all collections, whereas the smallest ripe females each year were at 150–159 mm or longer. For the combined spawning samples, 24.5% of the males were less than 160 mm long, as compared with only 9.2% of the females.

Although males and females were about equally represented in the annual trawl collections (the presence of more females among the larger alewives compensated for the earlier recruitment of males), sex ratios in the individual samples varied somewhat by season, depth, and vertical level. These variations appeared in the widespread collections of 1965 and 1966. In November, females made up 66–69% of the larger alewives in deep water but only 51–52% in shallow water. In July and August 1965, 56–57%

TABLE 3. Numbers of alewives of various lengths taken at different depths in gillnets of 1¼-inch (3.2-*cm*) mesh fished obliquely, 150 ft (45.7 *m*) per 20 ft (6.1 *m*) of fall, from surface to bottom[a], Saugatuck, Mich., May, July, and November 1962.

Date and total length (*mm*)	Depth interval (*ft*; *m* in parentheses)								
	0–20 (0–6.2)	21–40 (6.3–12.3)	41–60 (12.4–18.4)	61–80 (18.5–24.5)	81–100 (24.6–30.6)	101–120 (30.7–36.7)	121–140 (36.8–42.8)	141–160 (42.9–48.5)	Total[b]
May 23									
120–129	1	0	0	1	–	–	–	–	2
130–139	19	2	2	0	–	–	–	–	23
140–149	25	1	3	0	–	–	–	–	29
150–159	9	2	2	0	–	–	–	–	13
160–169	5	0	2	0	–	–	–	–	7
170–179	0	0	1	0	–	–	–	–	1
180–189	2	0	0	0	–	–	–	–	2
Total	61	5	10	1	–	–	–	–	77
July 6									
120–129	1	0	0	0	0	0	0	0	1
130–139	6	0	0	0	0	0	0	0	6
140–149	17	1	0	0	0	0	0	0	18
150–159	6	0	0	0	0	0	0	0	6
160–169	3	1	0	0	0	0	0	0	4
170–179	1	1	0	0	0	0	0	0	2
180–189	1	0	0	0	0	0	0	0	1
190–199	0	1	0	0	0	0	0	0	1
Total	35	4	0	0	0	0	0	0	39
November 6									
80–89	0	1	0	0	0	0	0	0	1
120–129	7	12	2	2	6	0	0	0	29
130–139	12	36	12	8	22	7	1	4	102
140–149	3	24	5	7	11	4	2	1	57
150–159	2	11	7	10	5	6	1	0	42
160–169	0	1	1	3	5	4	1	3	18
170–179	1	1	0	4	0	1	1	2	10
180–189	0	2	0	3	1	0	1	2	9
190–199	0	2	0	0	1	0	0	0	3
Total	25	90	27	37	51	22	7	12	271

[a]Bottom depths averaged 13 fathoms (23.8 *m*) May 23, and 26 fathoms (47.6 *m*) July 6 and November 6.
[b]Modal groups comprised mainly 2-year-old alewives in May and July and yearlings in November.

of the alewives in midwater collections were females, in comparison with 48–51% in the bottom collections at 3–14 fathoms (5.5–25.6 m). Females held a slight advantage (51–53%) in the combined spring, summer, and fall bottom collections of 1965 and 1966.

In contrast to the nearly equal sex ratios in the bottom collections, males greatly outnumbered

TABLE 4. Average lengths (*mm*) of adult alewives taken in experimental trawls at various bottom depths off Saugatuck, Mich., in April and November 1964–66.

	1964				1965				1966			
	Apr.		Nov.		Apr.		Nov.		Apr.		Nov.	
Depth (*fathoms*)	No. fish	Avg length	No. fish	Avg length	No. fish	Avg length	No. fish	Avg length	No. fish	Avg length	No. fish	Avg length
3	139	171	9	170	0	–	202	166	62	172	188	165
5	135	174	101	158	0	–	180	166	132	169	306	162
7	94	166	29	161	0	–	110	163	133	166	510	164
10	110	165	196	166	0	–	193	165	109	168	365	161
12	172	167	131	156	0	–	116	166	122	168	281	165
15	137	162	105	157	18	177	122	167	164	163	323	164
17	126	160	96	161	92	171	126	172	123	166	232	166
20	188	163	152	163	75	169	118	168	320	168	172	167
25	13	169	106	171	76	168	110	172	121	168	235	168
30	13	167	34	179	24	167	116	171	49	164	219	169
35	141	166	52	180	108	166	152	178	21	167	84	172
40	15	181	56	187	198	168	143	179	10	166	141	174
45	83	158	49	186	136	166	146	182	103	161	0	–
50	12	164	28	186	174	163	32	180	101	159	0	–
Total or mean	1378	166	1144	166	901	167	1866	170	1570	166	3056	165

TABLE 5. Percentage females in different length groups of alewives taken in experimental trawls, Saugatuck, Mich., and in trawls and from filtration plant screens, Chicago Harbor, 1965–66.

	Saugatuck[a]				Chicago[b]		Location and years combined	
	1965		1966		1966			
Total length (*mm*)	No. fish	% female	No. fish	% female	No. fish	% female	No. fish	% female
100–119	29	41	3	100	6	50	38	47
120–139	57	46	56	41	42	36	155	41
140–149	196	35	236	27	92	22	524	29
150–159	473	37	1042	27	368	28	1883	30
160–169	682	46	1701	49	610	47	2993	48
170–179	451	61	1348	65	435	64	2234	64
180–189	235	77	538	84	201	83	974	82
>189	112	88	177	90	73	84	362	88
Total	2235	51	5101	53	1827	51	9163	52

[a]April, July, August, and November 1965–66 and June 1966 at depths of 3–50 fathoms (5.5–91.5 *m*).

[b]Samples from the trawl catch in April (409 fish) and from the intake screens in April, May, and June (1418 fish).

females in the collections of spawning alewives from the rivers (Table 6). Since each spawning female was usually accompanied by a number of males, the males may spawn more frequently than the females, be more active on the spawning grounds, or remain on the spawning grounds longer than females.

Age and Growth

Age Structure of the Population

Alewives in Lake Michigan have the short life span that is especially characteristic in freshwater populations of this species. Less than 1% of those taken by trawl in 1964–70 were more than 6 years old (Table 7); however, several females in their ninth year of life in April 1968 and 1970 were at the maximum age previously reported from the Great Lakes (Graham 1956). The later recruitment and lower mortality rates of females (as compared with males) were reflected in the greater average age of females in spring and fall collections of all years (Table 7).

The abbreviated age structure changed substantially in southeastern Lake Michigan after the alewife population crested in the mid-1960s and was then decimated by the 1967 die-off (Table 7). Strong recruitment to adult stocks that generated the population upsurge was followed by poor recruitment after the die-off. Adult alewives appeared to live longer at the lower population densities in 1967–70 and, as indicated later, the age of maximum availability to trawls increased. As a result of these various changes, the dominant age-groups of males and females in the spring samples increased from III or IV in 1964 and 1965 to V in 1969 and 1970, and the average ages increased from 3.5–3.8 to 4.4–5.0 years. Changes were similar but less marked in the fall collections.

The altered age structure of alewives in Lake Michigan proper affected age distribution in the river spawning aggregations (Table 8). The numerically strongest age-groups of males from the Kalamazoo River were III and IV in 1965, and IV and V in 1970; in the same period, the average ages of the males and of the few females in the spawning aggregations increased from 3.3 to 4.6 years and from 3.7 to 5.0 years, respectively. Comparatively old alewives were predominant in the spawning samples from the St. Joseph River as well as from the Kalamazoo in 1968–70, and there was generally good agreement in age composition among fish from the two spawning areas.

The uniformity of age composition among alewives at six trawling locations from Benton Harbor, Mich., north to Sturgeon Bay, Wis., May 25–30,

TABLE 6. Length–frequency distribution of male (M) and female (F) spawning alewives taken in dipnets at night from the Kalamazoo River, Saugatuck, Mich., and the St. Joseph River, Benton Harbor, Mich., 1965–66 and 1968–70[a].

Total length (*mm*)	Kalamazoo River										St. Joseph River						Combined			
	1965		1966		1968		1969		1970		1968		1969		1970		No.		Cumulative %	
	(M)	(F)	(M)	(F)	(M)	(F)	(M)	(F)	(M)	(F)	(M)	(F)	(M)	(F)	(M)	(F)	(M)	(F)	(M)	(F)
110–119	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–[b]	–
120–129	2	–	2	–	–	–	1	–	–	–	–	–	–	–	–	–	5	–	0.3	–
130–139	5	–	4	–	2	–	1	–	2	–	2	–	–	–	14	–	30	–	1.6	–
140–149	46	–	34	–	14	–	2	–	4	–	22	–	2	–	23	–	147	–	8.3	–
150–159	85	5	119	9	24	3	9	1	7	–	56	8	32	–	23	–	355	26	24.5	9.2
160–169	108	9	198	20	74	9	18	–	14	1	145	8	52	2	49	2	658	51	54.5	27.1
170–179	58	13	96	23	73	17	19	2	39	3	127	20	89	6	97	2	598	86	81.7	57.4
180–189	14	9	32	11	16	17	12	2	42	3	53	15	54	16	70	2	293	75	95.1	83.8
190–199	4	2	3	2	6	13	3	3	15	2	13	3	13	7	40	5	97	37	99.5	96.8
200–209	1	1	–	1	–	1	–	–	2	–	–	3	–	1	8	1	11	8	100.0	99.6
210–219	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	100.0
Total	323	39	488	66	209	60	65	9	126	9	418	57	242	32	324	12	2195	284	–	–
Avg length	161	173	164	171	168	180	169	186	176	181	168	176	173	184	173	185	168	177	–	–

[a]Date collected: Kalamazoo River, July 8 1965, June 14–July 12 1966, June 15 and July 3 1968, July 1–2 1969, and June 30 1970; St. Joseph River, June 14 and July 2 1968, and July 1 1969 and 1970.

[b]Less than 0.05; one fish, the smallest ripe male (119 *mm*) in the spawning collections.

1968, indicated that age structure throughout Lake Michigan was controlled by the same conditions in the 1960s, and that the changes in southeastern Lake Michigan were representative of changes in other areas. Age-group IV alewives of the 1964 year-class dominated all collections over this large area 1 year after the lakewide die-off in 1967; they made up an average of 42% of the alewives collected in the northern part of the lake and 43% in the southern part. Age-V and older alewives were not

TABLE 7. Percentage age composition of male (M) and female (F) alewives taken in experimental trawls at Saugatuck, Mich., in fall (late October or November) and spring (April), 1964–70.

Season and sex	No. of fish	Age-group									Avg age (*years*)
		0	I	II	III	IV	V	VI	VII	VIII	
Fall											
1965											
(M)	44	–	–	47.7	47.7	4.6	–	–	–	–	2.6
(F)	71	–	–	22.5	66.2	11.3	–	–	–	–	2.9
1966											
(M)	120	–	2.5	37.5	49.2	10.8	–	–	–	–	2.7
(F)	136	–	2.2	18.4	61.8	16.9	0.7	–	–	–	3.0
1967											
(M)	188	–	2.6	36.2	46.3	14.9	–	–	–	–	2.7
(F)	155	–	2.6	12.9	56.1	26.5	1.9	–	–	–	3.1
1968											
(M)	157	–	3.2	14.7	41.4	33.1	7.0	0.6	–	–	3.3
(F)	117	–	4.3	8.5	22.2	45.3	15.4	3.4	0.9	–	3.7
1969											
(M)	95	–	17.9	11.6	22.1	33.7	12.6	2.1	–	–	3.2
(F)	80	1.2	21.3	5.0	12.5	30.0	20.0	8.8	1.2	–	3.5
1970											
(M)	110	–	16.4	10.0	18.2	34.5	20.0	0.9	–	–	3.3
(F)	116	–	18.1	9.5	5.2	24.2	31.0	10.3	1.7	–	3.8
Mean											
(M)	–	–	–	7.1	26.3	37.5	21.9	6.6	0.6	–	3.0
(F)	–	0.2	8.1	12.8	37.3	25.7	11.5	3.8	0.6	–	3.3
Spring											
1964											
(M)	93	–	–	–	57.0	37.6	5.4	–	–	–	3.5
(F)	94	–	–	–	45.7	45.7	7.5	1.1	–	–	3.6
1965											
(M)	95	–	–	3.2	52.6	40.0	3.2	1.0	–	–	3.5
(F)	87	–	–	2.3	37.9	43.7	14.9	1.2	–	–	3.8
1966											
(M)	69	–	–	4.4	44.9	44.9	5.8	–	–	–	3.5
(F)	111	–	–	1.8	27.0	51.4	18.9	0.9	–	–	3.9
1967											
(M)	127	–	–	3.1	50.4	40.2	5.5	0.8	–	–	3.5
(F)	187	–	–	0.5	24.1	55.1	18.2	2.1	–	–	4.0
1968											
(M)	152	–	–	11.8	24.3	46.1	14.5	2.6	0.7	–	3.7
(F)	143	–	–	14.0	8.4	37.8	32.8	4.9	1.4	0.7	4.1
1969											
(M)	149	–	–	3.4	13.4	34.9	40.3	6.7	1.3	–	4.4
(F)	158	–	–	2.5	3.2	13.3	56.3	21.5	3.2	–	5.0
1970											
(M)	132	–	–	1.5	8.3	37.1	47.0	6.1	–	–	4.5
(F)	138	–	–	–	2.2	18.1	55.8	22.5	0.7	0.7	5.0
Mean											
(M)	–	–	–	–	3.9	35.8	40.1	17.4	2.5	0.3	–	3.8
(F)	–	–	–	–	3.0	21.2	37.9	29.2	7.8	0.8	0.1	4.2

TABLE 8. Percentage age composition of spawning alewives taken at night with dip nets from the Kalamazoo River, Saugatuck, Mich., and the St. Joseph River, Benton Harbor, Mich., 1965 and 1968–70.

River and date	Sex	No. of fish	Age-group II	III	IV	V	VI	VII	VIII	Avg age (*years*)
Kalamazoo[a]										
July 8, 1965	(M)	176	10.2	48.9	38.1	2.8	–	–	–	3.3
	(F)	19	10.5	26.3	47.4	15.8	–	–	–	3.7
June 15 and July 3, 1968	(M)	209	5.7	11.5	45.0	34.0	3.8	–	–	4.2
	(F)	60	3.3	5.0	20.0	55.0	15.0	1.7	–	4.8
July 1–2, 1969	(M)	65	4.6	26.2	20.0	43.1	4.6	1.5	–	4.2
	(F)	9	–	22.2	11.1	33.4	22.2	11.1	–	4.9
June 30, 1970	(M)	124	6.5	7.3	32.3	30.6	16.9	5.6	0.8	4.6
	(F)	9	–	–	44.5	22.2	22.2	11.1	–	5.0
St. Joseph June 14 and July 2, 1968	(M)	286	6.0	10.9	45.1	33.9	3.8	0.3	–	4.2
	(F)	37	5.4	10.8	40.6	35.1	8.1	–	–	4.3
July 1, 1969	(M)	241	0.8	19.5	29.1	42.3	7.5	0.8	–	4.4
	(F)	31	–	–	29.0	54.9	12.9	–	3.2	4.9
July 1, 1970	(M)	179	15.0	12.3	30.2	24.6	16.2	1.7	–	4.2
	(F)	8	–	12.5	37.5	50.0	–	–	–	4.4

[a]Scales were not taken in 1966, but length composition was similar to that in 1965 and age composition is presumed to have been similar.

represented as well in the north (25% of fish) as in the south (34%) in 1968, but it is not known if natural mortality was greater in the north or if the fishery in Green Bay and adjacent areas affected population structure in northern areas, especially those as distant as Ludington.

LENGTH OF GROWING SEASON

The short growing season for alewives in cold, oligotrophic Lake Michigan began in late June (rarely May), July, or August depending on age and maturity; in general, growth began progressively later with increasing age of the fish (Table 9). Most yearlings began to grow in late June or July, but some adults that were in poor condition from spawning (late May to early August) did not grow before mid-August. Among yearlings collected off Waukegan in 1968, marginal scale growth was not evident in 49 of 50 fish collected June 15, but was slight to substantial in 42 of 47 collected July 29 and August 1. All of 12 yearlings collected at Saugatuck July 11, 1965, had new scale increments, in agreement with observations by Norden (1967). The percentages of age-II and older alewives with new annuli in 1965 and 1966 (data combined) were 4% near mid-June, 17% in early July, 44% in late July, and 86% near mid-August (Table 9). Seasonal growth was completed by late October and November, when the mean lengths for well-represented year-classes at various ages averaged about the same as in the following April.

CHANGES IN GROWTH RATE 1957–70

Detection of growth changes possibly related to the unusual population changes in Lake Michigan was the main objective of the growth analyses.

TABLE 9. Percentages of alewives of various ages with completed annuli among fish collected on different dates in experimental trawls at 3–7 fathoms (5.5–12.8 m), Saugatuck, Mich., 1965–66 (numbers of fish in parentheses).

Date	Age-group II	III	IV	All ages
May 23–24, 1966	0(4)	1(67)	0(45)	1(116)
June 14, 1966	12(8)	5(92)	0(48)	4(148)
July 11, 1965	41(22)	16(147)	8(40)	17(209)
Late July[a]	79(38)	48(125)	5(45)	44(208)
Mid-August[b]	100(72)	83(82)	31(13)	86(167)

[a]July 28, 1965, and July 23, 1966.
[b]August 14, 1965, and August 12, 1966.

Changes in growth could affect other population characteristics of alewives and indicate the severity of their ecological effects on the lake. All age-groups were combined to construct growth histories of the various year-classes because the calculated lengths did not change significantly with differences in the age of fish at capture. The sexes were treated separately, however, because females characteristically grow faster than males (Pritchard 1929; Havey 1961; and Norden 1967); in Lake Michigan, females gained their greatest length advantage during the third year. General growth based on the lengths calculated for the year-classes (Table 10) agreed reasonably well with that described by Norden (1967) for Lake Michigan alewives of ages I–IV (he did not age older fish).

Evidence from alewives taken in commercial poundnets in Green Bay in 1957–58 (Joeris and Karvelis MS 1962) indicated that growth was much faster during early establishment of the species in Lake Michigan. Calculated lengths of alewives taken with commercial gillnets (2½-inch or 6.4-cm mesh) in southeastern Lake Michigan in December 1958 also indicated a higher growth rate than that in recent years, although the nets may have caught the faster-growing fish. Average lengths of age-II alewives in the 1958 samples were not reached until age IV or older in the mid-1960s (Fig. 2).

As alewives became increasingly abundant in southeastern Lake Michigan in the 1960s, growth in the fourth, fifth, and possibly later years of life dropped substantially (Table 11). Length increments of both sexes were below the 1962–69 averages in 1963–66. Growth then rose appreciably to a 5-year high (1963–67) in 1967, seemingly in response to the extensive die-off in early 1967. Growth at age II, when many alewives are first recruited into bottom stocks from midwater, did not respond as markedly to the heavy mortality, and there was little if any effect on growth at age I. Declining growth of age-II alewives after 1967 may reflect competition for food and space with younger alewives of the strong 1968 and 1969 year-classes. Growth changes in other regions of the lake were probably equivalent to those in southeastern Lake Michigan, since calculated lengths were highly uniform among fish from six widely separated localities in May 1968. Average lengths of both males and females at the end of the

TABLE 10. Calculated total lengths (*mm*) at the end of successive years of life for male (M) and female (F) alewives of the 1958–68 year-classes from combined trawl and dipnet collections at Saugatuck, Mich., 1964–70 (numbers of fish in parentheses)[a].

		End of year of life							
Year-class	Sex	1	2	3	4	5	6	7	8
1958	(F)	102(1)	149(1)	168(1)	182(1)	192(1)	193(1)	–	–
1959	(M)	102(6)	149(6)	169(6)	182(6)	188(6)	194(1)	–	–
	(F)	106(8)	154(8)	176(8)	188(8)	193(8)	211(1)	–	–
1960	(M)	102(43)	146(43)	161(43)	169(43)	178(8)	–	–	–
	(F)	100(61)	147(61)	168(61)	177(61)	187(18)	207(2)	219(1)	228(1)
1961	(M)	99(166)	144(166)	159(166)	169(113)	179(8)	180(2)	191(1)	–
	(F)	97(128)	142(128)	162(128)	175(85)	184(38)	187(9)	189(4)	206(1)
1962	(M)	97(225)	143(225)	159(225)	169(89)	174(37)	182(17)	187(5)	197(1)
	(F)	98(226)	147(226)	166(226)	176(188)	183(84)	190(27)	196(11)	196(2)
1963	(M)	98(300)	144(300)	159(300)	169(248)	175(138)	184(34)	190(9)	–
	(F)	99(397)	145(397)	164(397)	173(351)	182(164)	190(64)	200(11)	195(2)
1964	(M)	97(507)	142(507)	158(507)	167(398)	176(182)	185(42)	190(1)	–
	(F)	97(362)	142(362)	163(362)	175(337)	183(206)	195(61)	204(12)	–
1965	(M)	97(389)	144(389)	160(389)	170(282)	179(152)	186(22)	–	–
	(F)	97(219)	144(219)	165(219)	177(187)	185(140)	194(36)	–	–
1966	(M)	98(209)	145(209)	160(209)	171(149)	178(38)	–	–	–
	(F)	99(84)	148(84)	165(84)	177(67)	184(28)	–	–	–
1967	(M)	99(51)	146(51)	160(51)	172(20)	–	–	–	–
	(F)	100(9)	151(9)	168(9)	172(6)	–	–	–	–
1968	(M)	92(11)	135(11)	155(11)	–	–	–	–	–
	(F)	94(11)	142(11)	159(11)	–	–	–	–	–
Mean	(M)	98(1907)	144(1907)	159(1907)	169(1348)	177(569)	184(118)	189(16)	197(1)
	(F)	98(1506)	144(1506)	164(1506)	175(1291)	183(687)	192(201)	199(39)	203(6)

[a]Age II excluded in spring and summer because of size selection in some years.

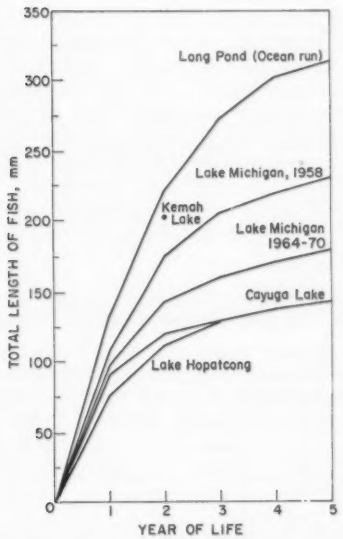

FIG. 2. Annual growth of alewives in fresh and salt water. Sources of outside data were: Lake Hopatcong and Kemah Lake, N. J., length frequencies, Gross (MS 1959); Cayuga Lake, N.Y., length frequencies and lengths of age groups at capture, Rothschild (1965); and Long Pond, Me., back calculations, Havey (1961).

first 5 years of life at the southern localities (Benton Harbor, Saugatuck, and Grand Haven) were within ± 1 mm of those at the northern localities (Ludington, Manitowoc, and Sturgeon Bay).

The likelihood that changes in population density affected the growth of alewives in Lake Michigan is supported by a discovery made by Wells (1970) of changes in zooplankton. Wells believed that overabundant alewives selectively cropped and depleted larger plankton species, which have made a partial recovery since the 1967 die-off. Brooks (1968), who studied the effects of size-selective predation by alewives on zooplankton in other lakes, reported that alewives are obligate planktivores and shift to progressively smaller zooplankters as large ones become scarce. The probability that large alewives are more dependent than small alewives on the larger zooplankton may explain why the major growth changes were among the older fish in Lake Michigan. In Birch Lake, Michigan, the growth of lake herring, which fed primarily on zooplankton (G. N. Washburn personal communication), was similarly affected after the second year of life by changes in population density (Clady 1967).

The probable direct relation between changes in growth of alewives in Lake Michigan and their selective depletion of the zooplankton may explain the wide range in growth reported for the species

TABLE 11. Percentage deviation of annual length increments of male (M) and female (F) Lake Michigan alewives from the 1962–69 means for the second through fifth years of life (numbers of fish in parentheses).

	Year of life							
	2		3		4		5	
Year	(M)	(F)	(M)	(F)	(M)	(F)	(M)	(F)
1962	−1.5	−2.6	−3.2	10.3	51.7	18.0	35.1[a]	31.6
	(166)	(128)	(43)	(61)	(6)	(8)	(–)	(1)
1963	0.2	1.3	−3.2	6.2	−12.6	−20.0	−22.1	−32.9
	(225)	(226)	(166)	(128)	(43)	(61)	(6)	(8)
1964	0.4	−1.9	4.5	0.0	−16.1	−14.0	−10.4	−38.2
	(300)	(397)	(225)	(226)	(113)	(85)	(8)	(18)
1965	−2.2	−2.3	0.0	−2.6	−10.3	−15.0	−23.4	−14.5
	(507)	(362)	(300)	(397)	(89)	(188)	(8)	(38)
1966	2.6	−0.7	3.9	6.2	−10.3	−7.0	−10.4	−10.5
	(389)	(219)	(507)	(362)	(248)	(351)	(37)	(84)
1967	3.5	1.9	7.1	9.2	9.2	19.0	16.9	23.7
	(209)	(84)	(389)	(219)	(398)	(337)	(138)	(164)
1968	2.4	4.1	−3.2	−13.8	9.2	18.0	16.9	19.7
	(51)	(9)	(209)	(84)	(282)	(187)	(182)	(206)
1969	−5.9	0.4	−7.7	−16.4	8.0	5.0	0.0	15.8
	(11)	(11)	(51)	(9)	(149)	(67)	(152)	(140)

[a]Estimated by proportion from the fourht-year increment of 1962 and the fourth- and fifth-year increments of 1963.

in various fresh waters (Fig. 2). The small size of zooplankters in Cayuga Lake, New York, suggested size-dependent predation (Brooks and Dodson 1965), and growth of alewives was poorer there in the early 1960s than in Lake Michigan. Growth of alewives in 2657-acre (1076-ha) Lake Hopatcong, New Jersey, is among the poorest on record, whereas in some sand pits and ponds in New Jersey such as 108-acre (43.7-ha) Kemah Lake, growth in the early years of life approached that in salt water (Gross 1953, MS 1959). Gross noted that alewives may grow faster in the ponds because productivity in the ponds is higher than in the lakes.

Although a sparser planktonic food supply may depress growth in Lake Michigan and other fresh waters as compared to that in the Atlantic Ocean (Fig. 2), other conditions may also contribute to the differences in growth. Hoar (1952) proposed that growth of alewives in fresh water may be limited by osmoregulatory demands on the thyroid mechanism, and Graham (1956) suggested that excess thyroid activity may hasten sexual maturity and indirectly depress growth in fresh water. On the other hand, Stanley and Colby (1971) reported that alewives adapted to sea water exhibited no clear advantage over those adapted to fresh water when placed under acute temperature stress; and unstressed alewives were seemingly excellent osmoregulators in both fresh and salt water. Gross (MS 1959) also noted that both slow- and fast-growing populations in New Jersey matured in the second year of life. Perhaps more severe temperature regimes than in the ocean and adverse physiological effects of low temperature (Colby 1972) are the central causes for the apparent depression of growth rate in fresh water.

Changes in Weight 1965-70

Average weights of alewives in southeastern Lake Michigan changed by season in 1965 and 1966. Weight was high in spring and fall and lowest in midsummer (Fig. 4). The weight loss in summer represented a true decline in condition, as well as a loss of sex products during the spawning season. Alewives are known to stop feeding after they enter rivers to spawn (Cooper MS 1961), and thin, emaciated fish were conspicuous in the summer bottom collections from Lake Michigan. The midsummer decline in weight in 1965 and 1966 was greater and more consistent for males than for females; females were heavier than males in all the monthly collections (Fig. 3).

As indicated by weights averaged over a standard range of lengths, the condition of alewives, as well as their growth rate, appears to have been affected by

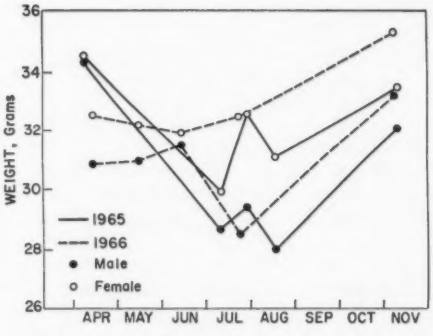

FIG. 3. Seasonal changes in body weight of Lake Michigan alewives at Saugatuck, Mich., 1965–66. Points are unweighted means of average weights in 5-mm length intervals from 150–154 mm through 185–189 mm.

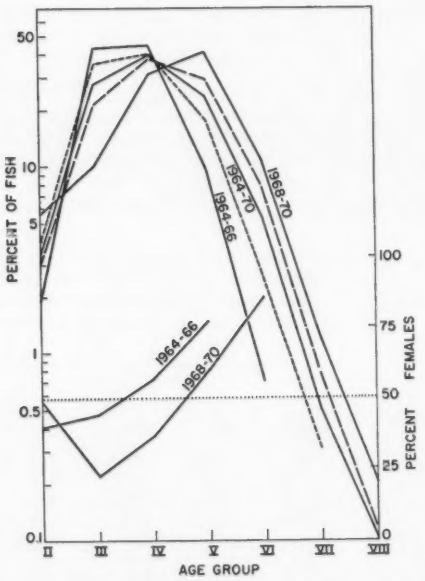

FIG. 4. Changes in average age–frequency distribution (five upper curves; scale at left) and in the relation between percentage females and age (two lower curves; scale at right) of alewives taken in trawls off Saugatuck, Mich., in April during different years 1964–70. Broken lines show separate age frequencies for males (short dashes) and females (long dashes) for the entire period 1964–70; solid lines represent combined sexes for 1964–66 (before the 1967 die-off), 1968-70 (after the die-off), and 1964–70 (the entire period of study). The dotted line aids in identifying the ages at which the percentage females in bottom stocks reached 50%, before and after the die-off.

population density in the 1960s; and furthermore, condition apparently was an important factor in survival. Average weights over the standard length range were poor when adult alewives were extremely abundant in 1965, 1966, and the spring of 1967, but were markedly improved in the fall of 1967 and in 1968, 1969, and 1970 (Table 12). The mass mortality of 1967 (June–July) clearly separated the two periods of strikingly different body condition. Mean index weights of males in the fall samples increased 26% from 1966 to 1967 and the weights of females increased 16%. The respective mean weights for males and females in the spring collections of 1968 improved 19 and 18% over those of 1967.

That the poor condition of November 1966 was followed by severe winter mortality was first revealed by the collection of large numbers of dead alewives in advanced stages of decomposition, in early April 1967 at deeper trawling depths (35–50 fathoms; 64.0–91.5 m) off Grand Haven, Saugatuck, and

TABLE 12. Annual changes in the weight (*g*) of male (M) and female (F) alewives in spring and fall trawl collections from Saugatuck, Mich., 1965–69: horizontal rules separate collections made before and after the June–July 1967, die-off.

Season, sex, and year	No. of fish	Avg length (*mm*)	Weight–length relation (base 10 log)		Covariance		Mean wt[c]	% wt increase
			Intercept	Slope[a]	Adjusted mean log-wt	Test of differences[b]		
Fall								
(M)								
1965	47	166	–3.44	2.12	1.4673	NS	33.8	–
1966	230	164	–3.35	2.18	1.4839		33.8	–
1967	201	168	–4.68	2.82	1.6000		42.5	26
1968	167	170	–4.70	2.83	1.6084	S	43.0	–
1969	84	171	–4.58	2.76	1.5730		39.2	–
1970	111	169	–3.94	2.47	–	–	38.6	–
(F)								
1965	77	175	–2.80	1.94	1.5316	NS	33.6	–
1966	277	172	–2.97	2.02	1.5530		35.6	–
1967	180	178	–4.08	2.54	1.6453		41.2	16
1968	134	180	–4.39	2.69	1.6652	S	42.9	–
1969	81	177	–4.86	2.88	1.6282		40.1	–
1970	119	178	–3.53	2.29	–	–	39.0	–
Spring								
(M)								
1965	103	166	–3.00	2.03	1.4977		34.5	–
1966	193	166	–3.27	2.13	1.4554	S	31.6	–
1967	127	162	–4.24	2.57	1.4569		32.8	–
1968	153	163	–5.19	3.03	1.5404	NS	38.9	19
1969	156	170	–4.90	2.90	1.5456		39.1	–
1970	230	172	–4.60	2.76	–	–	37.2	–
(F)								
1965	95	171	–3.37	2.20	1.5484	NS	35.6	–
1966	260	173	–3.11	2.07	1.5225		33.5	–
1967	187	173	–3.59	2.28	1.5167		32.9	–
1968	144	170	–5.15	3.01	1.6164	NS	38.9	18
1969	163	182	–5.15	3.01	1.6171		39.3	–
1970	266	185	–4.44	2.69	–	–	37.6	–

[a]Slopes differed significantly in four comparisons ($P \leq 0.01$) with the samples of 1965–69 grouped together, but not in eight comparisons ($P > 0.05$) of the subgroups separated by the June–July 1967 mortality.

[b]Differences among the adjusted means within the eight subgroups were either not significant, NS ($P > 0.05$); or significant, S ($P \leq 0.01$).

[c]Unweighted mean of the average weights of alewives in the 160–164 through 180–184 mm length intervals.

Benton Harbor. Evidence of winter mortality was negligible in April 1968 and 1969, after relatively mild winters, but a sizable winter die-off developed in both southern and northern areas in the winter of 1969–70, which was the coldest since 1962–63 (Colby 1972). Many alewives died in 1969–70 despite the only moderate abundance of adults and their comparatively good condition in the fall of 1969. Appreciable mortalities continued into April and May 1970; however, the die-off was far less extensive than that of 1967.

This sequence of events in Lake Michigan indicates that poor condition resulting from high population density made alewives more susceptible to low-temperature stress and greatly increased the intensity of the 1967 mortalities, but that low temperature is alone sufficient to cause die-offs in some years, as indicated also by Colby (1972) on the basis of field observations and related laboratory experiments. The condition of alewives in fall seems especially important for survival, since Colby's experiments showed that alewives are less tolerant of low temperatures than some native species. Good condition in fall apparently not only improved survival during the following winter but also led to good condition in spring, which in turn may have strongly increased the resistance of alewives to environmental stresses that trigger the frequent spring and early summer mortalities.

Improvement in the condition of alewives after the mass mortality of 1967 produced consistent changes in the weight–length relation (Table 12). Slopes of the least squares regression lines (logarithms of weights and lengths) for males and females in the spring and fall collections were substantially greater after the die-off, indicating relatively greater weight improvement for the larger alewives. A slope of three, which was closely approximated by Atlantic Ocean alewives measured in fork length (Cooper MS 1961), was slightly exceeded by Lake Michigan alewives in several collections made after 1967. Slope differences among the weight–length regressions of 1965–69 were significant ($P \leq 0.01$) in each of four comparisons by sex and season, but were not significant in any of eight comparisons when alewives collected before and after the mass mortality of 1967 were tested separately (Table 12). Although mean log-weights adjusted by covariance differed statistically in three of the eight subgroups and seasonal differences may have been significant, the weights from the various years (exclusive of 1970 weights obtained later) and seasons within the two periods separated by the 1967 die-off were pooled and averaged by 5-mm length intervals to yield the following general prediction equations:

Males, before die-off: $\text{Log } W = -3.29 + 2.16 \text{ Log } L$
Males, after die-off: $\text{Log } W = -4.90 + 2.91 \text{ Log } L$
Females, before die-off: $\text{Log } W = -3.52 + 2.26 \text{ Log } L$
Females, after die-off: $\text{Log } W = -5.12 + 3.01 \text{ Log } L$

Changes in Abundance and Population Structure 1949–70

The establishment of alewives in Lake Michigan and their changes in abundance and population structure were documented by field observations, experimental fishing, and analysis of commercial fishing statistics (Smith 1968; Brown 1968; Reigle 1969a).

Lakewide Establishment 1949–60

Alewives spread rapidly throughout Lake Michigan after 1949, when the first specimen (an adult) was collected near South Manitou Island (Miller 1957). Single adults were collected at White Lake, at Milwaukee, and in Green Bay in 1951–52 and at Chicago in 1954 (Miller 1957; Joeris and Karvelis MS 1962; and Woods 1960). Schools of young were first seen in Green Bay in 1954, in East Bay near Traverse City in 1955, and at Chicago in 1956. Experimental fishing by the *Cisco* at 6-year intervals indicated the rapidity of the population buildup. In 1954, none were caught at seven southern locations during 36 hr of bottom and midwater trawling, compared with 45,387 in 78 hr in 1960. Similarly, in 1955 only 8 were taken at five northern localities during 19 hr, compared with 38,439 in 42 hr in 1961. Increasingly larger numbers of dead alewives were seen near Chicago in 1957–60 (Woods 1960), and water intake screens were blocked for the first time at the Waukegan generating plant of Commonwealth Edison Co. in May 1961 (Danson 1967).

Unprecedented Abundance and the 1967 Die-Off

The adult population increased prodigiously in southern Lake Michigan in the 1960s (Table 13). The catch per unit of effort (CPE) for systematic assessment trawling in fall at Saugatuck increased fivefold from 1962 (86 fish per tow) to 1965 (433 per tow). Large increases in CPE (based on weight of fish) were also experienced by commercial trawlers (Table 14). The extremely high population density held through 1966. In this period, blockage of water intakes became critical. Tons of alewives were cleaned daily from intake screens at the Chicago Central District Filtration Plant at the peak of the inshore migration in the spring of 1965 and 1966, and nets were installed to divert alewives from the intake canal (Greenwood 1970).

TABLE 13. Number of adult (≥120 *mm*) and young-of-the-year alewives taken per 10-min tow of experimental trawls at 3–40 fathoms off Saugatuck, Mich., in late October or November, 1962–70.

Life stage and depth (*fathoms*)	Contour width (*miles*)	Nov. 8, 9 1962	Nov. 7, 9 1963	Nov. 4 1964	Nov. 10 1965	Nov. 15 1966	Nov. 10, 13 1967[a]	Nov. 3, 4 1968[a]	Oct. 29, 30 1969[a]	Oct. 24, 26 1970[a]
Adults										
3	0.4	294[b]	64	18	406	80	0	0	2	0
5	0.4	294	182	176	260	514	2	6	3	4
7	0.9	18	111	28	657	911	59	26	22	2
10	0.9	80	52	198	803	752	95	27	2	4
12	0.6	46[b]	62	238	497	429	122	51	4	31
15	0.6	12	107	308	507	534	180	39	35	44
17	0.5	110	42	204	798	805	111	14	33	92
20	0.8	26	74	396	507	529	75	106	38	190
25	1.0	57	206	106	227	400	77	88	66	140
30	1.1	76	60	34	232	219	96	54	174	164
35	1.6	182	14	52	156	84	144	40	258	240
40	3.4	1	12	56	143	141	438	38	205	126
CPE[c,d]	–	86	82	151	433	450	133	44	84	99
(Σ catch × miles)/10	–	87	76	144	420	439	234	54	146	138
Young of year										
3	0.4	7[b]	12	1714	2340	0	44	643	48	1005
5	0.4	7	254	1478	2638	4	585	1028	1116	2250
7	0.9	27	357	2599	2500	42	227	1882	2560	1226
10	0.9	48	25	107	946	587	44	2546	1826	4908
12	0.6	61[b]	78	319	925	518	16	1669	2247	1452
15	0.6	74	299	1591	22	320	133	4234	1128	52
17	0.5	30	204	1989	0	462	103	1760	1766	166
20	0.8	28	5	5863	0	2	51	216	4312	6
25	1.0	4	3	0	0	2	22	1	540	60
30	1.1	0	0	0	0	1	6	1	23	12
35	1.6	0	0	1	0	0	6	0	0	4
40	3.4	0	0	0	0	0	1	0	0	2
CPE[c]	–	31	137	1740	1562	215	112	1578	1557	969
(Σ catch × miles)/10[e]	–	20	78	1054	566	131	72	946	1134	790

[a]Data shown are 2-day averages; however, all catches were used to compute the CPE. The summation of catch times contour width is an average for the 2 days.

[b]Estimated from adjacent catches for inclusion in the summation of catch times contour width.

[c]Average catch per tow that took alewives.

[d]Index of abundance for adults.

[e]Index of abundance for young-of-the-year that occupied greater depths in years when the thermocline was deeper.

TABLE 14. Availability of alewives to experimental and commercial trawls in Lake Michigan off Saugatuck, Mich., and to commercial trawls from Two Rivers south to Kenosha, Wis., November 1960–70.

	Adjusted catch rate[a]			
		Commercial		
Year	Experimental	Mich.	Wis.	Mean
1960	–	–	14	14
1961	–	–	77	77
1962	100	100	100	100
1963	82	71	91	81
1964	143	266	151	187
1965	407	419	211	346
1966	417	449	350	405
1967	153	188	184	175
1968	55	–[b]	–[b]	55
1969	99	–[b]	–[b]	99
1970	117	–	–[b]	117

[a]Catch rates as percentages of the 1962 rates of 46 lb (21 kg)/hr for experimental trawling and 576 lb (261 kg) and 438 lb (199 kg)/hr for commercial trawling in Michigan and Wisconsin, respectively.

[b]Not valid for comparison because fishing power was markedly increased by changes in net design.

The uncommonly large numbers of dead alewives collected at the deeper trawling depths (35–50 fathoms; 64.0–91.5 m) off Grand Haven, Saugatuck, and Benton Harbor, Mich., in April 1967 signaled that the population was seriously overextended. The winter mortality and the heavy mortality that followed in June and early July contributed to a 70% drop in the index catch in 1967 (Table 13) and a heavy drop in the commercial catch rate (Table 14).

Despite uncertainty as to what physiological responses were immediately involved in the huge die-off (thermal shock may have been important), several developments linked the high mortality directly to high population density: the extremely high abundance before the die-off; changes in growth and condition; and the effects on zooplankton. The peak abundance of alewives in the mid-1960s was apparently beyond the carrying capacity of Lake Michigan and could not be sustained. Abundance of adult alewives in southeastern Lake Michigan was low after the die-off, judging by the much lower CPE's at Saugatuck (44–133 fish per tow, Table 13) and at Benton Harbor (82–134 fish per tow) during 1967–70. The average unweighted rate of catch for the combined fall index stations (Saugatuck, Benton Harbor, Ludington, and Waukegan) improved considerably from 1967–68 (116 per tow) to 1969 (184 per tow) and 1970 (295 per tow), mainly because of steady improvement at Ludington and Waukegan.

YEAR-CLASS STRENGTH

The 1962 and 1963 year-classes contributed more than earlier and later year-classes to the population increase in the mid-1960s, as determined by summation of the contributions at successive ages to the fall index catches at Saugatuck (Table 15). The 1964 year-class was also well represented in the index catch at age II in 1966, and although greatly reduced in the 1967 die-off, contributed substantially to the index catches through 1970. Alewives of the 1963 (age IV) and 1964 (age III) year-classes composed 34 and 50%, respectively, of the dead alewives sampled at five locations in June 1967 (Brown 1968). The strong early appearance of age I alewives of the 1968 and 1969 year-classes (16.8 per tow in 1969 and 17.1 in 1970) at Saugatuck (Table 15) and other areas indicated that the 1970 level of abundance may be maintained or possibly improved in the early 1970s.

MORTALITY AND AGE AT RECRUITMENT

Mortality, which changed markedly in the 1960s, was roughly measured by the percentages of alewives lost by individual year-classes from one fully recruited age-group to the next in the fall index catch at Saugatuck (Table 15). The losses in number per tow from age-group III to age-group IV during 1964–68 ranged from 40% in 1965 to 89% in 1967 and averaged 68%. Higher losses were indicated for some years from age-group IV to age-group V. During the mid-1960s alewives were fully recruited into bottom stocks and therefore available in maximum numbers to trawls near age III in the fall (they are never completely available because some remain pelagic). After 1968, however, alewives were not fully recruited until age IV or older (year-classes 1965 and 1966, Table 15). Mortality of older alewives (mainly V–VII) in the earlier year-classes apparently decreased at the lower population densities of 1968–70. As survival improved, the rate of capture of age-V alewives steadily increased from 1.2 per tow in 1967 (1962 year-class) to 25.4 per tow in 1970 (1965 year-class), and alewives through age VII were present in each of the fall collections in 1968–70 (Table 15). Increased survival of alewives during 1968–70 was also indicated by changes in slope at age IV or V in semilog curves (not shown) constructed from the catch rates of the 1961–64 year-classes. The change in slope indicating a drop in mortality was especially pronounced for the 1962 year-class.

Residence of alewives in midwaters until a greater age in the late 1960s than earlier was also evident in the age-frequency curves averaged for each age-group over the April collections of 1964–66 and 1968–70 and from changes in the percentage females at successive ages (Fig. 4). The development of a 50:50 sex ratio, indicating that recruitment of females into bottom stocks has mainly overtaken the earlier recruitment of males (also see Table 5), moved from between ages III and IV in 1964–66 to between ages IV and V in 1968–70. This shift indicates that a delay in the attainment of sexual maturity lengthened the stay at midlevels. Similarities in age composition between the bottom stocks and spawning alewives (Tables 7 and 8) and the differential recruitment of the sexes indicate that sexual maturation is indeed a factor in the time of descent from midlevels.

The age-frequency curve representing all of the April collections of 1964–70 (Fig. 4) reflects the high total mortality of adult alewives in southeastern Lake Michigan, confounded by the increase in age at recruitment into bottom stocks and by the changes in abundance. On the basis of the mean age frequencies, mortality after the fifth year of life for the sexes combined was tentatively estimated by the Jackson (1939) method as 80% in April (1964–70) and 79% in October–November (1965–70). Havey (1961) estimated average mortality at 79% from age V to age VI for marine alewives that spawned in Long Pond, Maine.

Progeny–Parent Relations

Recruitment of the 1962–67 year-classes into bottom stocks at ages II to IV varied inversely with the abundance of adults in the fall preceding the year in which each year-class was spawned (Fig. 5). For example, a peak index catch of 391 recruits of

TABLE 15. Numbers of alewives contributed by the 1958–69 year-classes to the catch per unit of effort in experimental trawls at Saugatuck, Mich., in late October or November, 1962–70 (age is shown in parentheses).

Year-class	Age-0 abundance index	Year of capture									Sum of age II and older	% change age III to IV
		1962[a]	1963[b]	1964[b]	1965	1966	1967	1968	1969	1970		
1958	–	–	0.5 (V)	–	–	–	–	–	–	–	–	–
1959	–	–	5.2 (IV)	1.6 (V)	–	–	–	–	–	–	–	–
1960	–	22.8[c] (II)	34.2 (III)	13.3 (IV)	–	–	–	–	–	–	70	–0.61
1961	–	–	42.1 (II)	63.1 (III)	37.7 (IV)	1.8 (V)	–	0.2 (VII)	–	–	145	–0.40
1962	20	–	–	68.9 (II)	255.9 (III)	63.4 (IV)	1.2 (V)	0.7 (VI)	0.5 (VII)	–	391	–0.75
1963	78	–	–	4.1 (I)	139.4 (II)	251.6 (III)	26.7 (IV)	4.8 (V)	4.3 (VI)	0.8 (VII)	428	–0.89
1964	1054	–	–	–	–	122.8 (II)	67.4 (III)	17.7 (IV)	13.4 (V)	5.7 (VI)	227	–0.74
1965	566	–	–	–	–	10.4 (I)	34.2 (II)	14.5 (III)	26.9 (IV)	25.4 (V)	101	+0.84
1966	131	–	–	–	–	–	3.5 (I)	4.5 (II)	14.9 (III)	29.0 (IV)	48	+0.95
1967	72	–	–	–	–	–	–	1.6 (I)	7.2 (II)	11.4 (III)	–	–
1968	946	–	–	–	–	–	–	–	16.8 (I)	9.6 (II)	–	–
1969	1134	–	–	–	–	–	–	–	–	17.1 (I)	–	–
1960–64 average[d]		–	–	–	–	–	–	–	–	–	–	–0.68
Total CPE		86	82	151	433	450	133	44	84	99	–	–

[a]Scales not taken.
[b]Based on age composition of following April.
[c]Ratio estimate based on closest set of data.
[d]Later year-classes are excluded because they were not available in maximum numbers to trawls until after age III.

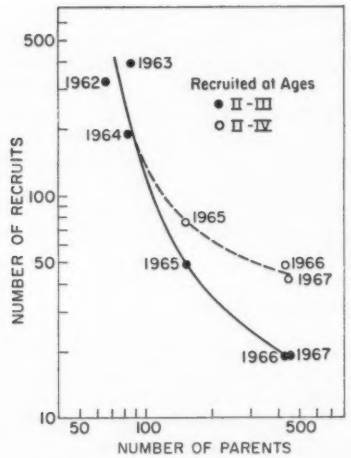

FIG. 5. Abundance of alewives of the 1962–67 year-classes upon recruitment into adult stocks in relation to abundance of adults (parents) in the fall preceding the respective spawning seasons in which they were produced, as indicated by trawl catches off Saugatuck, Mich. Parents of the 1962 year-class were estimated by proportion from the 1963 value and the November commercial catch rates in 1961 and 1962; age-IV recruits of the 1967 year-class were similarly estimated from age-III recruits and recruits of the same ages from the 1966 year-class. Curves fitted by inspection.

the 1963 year-class (at ages II–III) was associated with a low index catch of 86 adults in the fall of 1962, whereas an index catch of only 48 recruits of the 1966 year-class (at ages II–IV) was associated with a high index catch of 433 adults in the fall of 1965 (Table 15). The exact form of the underlying relation (the greater the number of parents, the weaker the recruitment) is uncertain because of the increased age at recruitment in 1968–70 and the resulting need for including age-IV alewives among recruits from the 1965–67 year-classes (Fig. 5).

Whether the progeny–parent relation for alewives stabilizes in Lake Michigan may depend upon the intensity of predation from large numbers of salmon and lake trout stocked since 1965–66 (Great Lakes Fishery Commission 1970) and from burbot, which are reported by fishermen to be recovering in some northern areas. As stocking of salmonids continues and predation increases, the extremely high population density of adult alewives that caused their poor condition in the mid-1960s is not likely to be repeated. It is roughly estimated that 6.5 million lb (2.95 million kg) of salmon and trout caught in 1969 at weirs and by commercial and sport fishermen in Michigan waters consumed 32–65 million lb (14.5–29.5 million kg) of alewives, and that the 1970 catch of 10 million lb (4.54 million kg) of salmonids consumed 50–100 million lb (22.7–45.4 million kg) (J. Bails, Michigan Department of Natural Resources, Lansing, personal communication). These preliminary estimates, made from the approximation that 5–10 lb (2.27–4.54 kg) of alewives consumed produce 1 lb (0.45 kg) of salmonid, account for only a small fraction of the lakewide trout population and none of the salmon caught in Indiana, Illinois, and Wisconsin waters. Although the estimates may be inflated somewhat because of the presence in the salmonid diet of other species such as smelt (*Osmerus mordax*) and sculpins (mainly *Cottus cognatus*), they indicate that mortality from predation may have surpassed fishing mortality (discussed in a later section) in 1970 and that predation is a significant factor in alewife survival.

A relation between abundance of young-of-the-year alewives and their parent stock, also represented by the relative abundance of adults in the fall preceding the spawning season, was indicated by abundance indices of the 1964–70 year-classes, except that of 1967 (Fig. 6). Additional data are needed to confirm this relation because of the high variability among the trawl catches of young alewives (Table 13). The young often ascend into midwaters during

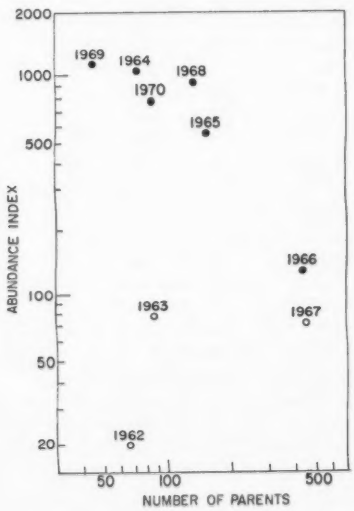

FIG. 6. Abundance of young-of-the-year alewives of the 1962–70 year-classes in relation to abundance of adults (parents) in the fall preceding the spawning seasons in which the respective year-classes were produced. Abundance of adults and young was based on fall trawl catches off Saugatuck, Mich. Open circles indicate questionable values.

turbulence from high winds in fall (Wells 1968), and the below-average size of the young in fall may further affect their index value. Also, since the depth to which the young range tends to be directly related to the depth of the thermocline, and this varies from year to year, a modified abundance index was used rather than the unmodified CPE used for adults (footnote, Table 13). Nevertheless, young-of-the-year of the strongest year-class (1969; abundance index 1134) came from the weakest parent stocks (1968; 44 fish per tow), and those of one of the weakest year-classes (1966; 131 fish per tow) came from the second strongest parent stocks (1965; 433 per tow); and abundance indices for young of the 1964–66 and 1968–70 year-classes tended to decline with an increase in the density of the parent stock (Table 15, Fig. 6).

Additional support for an inverse progeny–parent relation by abundance indices of the 1967 year-class and its parents (Fig. 6) is highly questionable because good catches of young-of-the-year were made during supplemental trawling at Saugatuck in mid-October 1967, preceding the very low index catch in November. In all other years, when both early and late trawling was conducted, the abundance indices for young alewives were lower in early and mid-October than in late October or November as shown below:

Year	Early to mid-October	Late October or November
1964	594	1054
1967	643	72
1968	730	946
1969	425	1134
1970	408	790

On the basis of the early fall index of 1967 (643) and the ratio of early to late fall indices in the other 4 years, an alternative abundance index of 1170 young-of-the-year is estimated for 1967. If accurate, this implies that high production of young alewives in 1967 may have resulted from a lower parent stock than is indicates by the late fall catch in 1966 (450 per tow), because the adults were subjected to high winter and spring mortalities before they spawned in 1967 (Brown 1968).

The low catches of young-of-the-year alewives during low parent stock densities in 1962–63 also had no apparent connection with the progeny–parent relation suggested in later years (Fig. 6). Either survival was exceptional in 1962 and 1963 or the young-of-the-year were grossly underestimated by the trawl catches, because the contributions of these two year-classes to adult stocks were stronger than those of any year-class in the 1960s (Table 15).

Excluding the unexplained low abundance indices of young-of-the-year in 1962–63 and the seemingly aberrant 1967 value, recruitment of the 1964, 1965, and 1966 year-classes to adult stocks at ages II and IV declined with a decrease in their earlier abundance as young-of-the-year, although the suggested positive correlation (1 degree of freedom) was not statistically significant ($r = 0.952$). Whether such a relation is eventually confirmed will be determined by the combined effects of the various limiting factors controlling the number of young that reach adult stocks in Lake Michigan. Competition for food and space among the numerous young in some years, between the young and adults, and between the young a ewives and the young of other species, particularly smelt and bloaters (Wells and Beeton 1963), may all influence survival. Environmental conditions such as the winter temperature regime apparently affect survival independently of abundance in some years (e.g., in the winter of 1969–70) and may mask any sharp relation between the young and later abundance as adults.

Young as well as adult alewives experienced noticeable mortalities in winter, spring, and summer of some years. Yearlings composed 28% of the dead alewives sampled in June 1967 (Brown 1968) and were present among alewives that died in the previous winter. They were also well represented among alewives that died in the winter and spring of 1969–70. Severe fin degeneration observed among many young alewives in trawl collections in November 1964–68 (Brown and Norden 1970) may also have caused mortality in those years. The chronic fin condition indicated that environmental conditions such as high summer temperatures and pathogens in shallow water were unfavorable in some areas of southern Lake Michigan.

The buildup of sizable populations of predators in Lake Michigan added a new dimension to the mortality of young alewives in the late 1960s. Immature lake trout (Wright MS 1968) and coho salmon (*Oncorhynchus kisutch*) are known to feed heavily on young-of-the-year and yearling alewives in seasons when they occupy the same locations; therefore, the estimated poundages of alewives consumed in Michigan waters have added significance. In fact, Wright (MS 1968) suggested that predation on the young is an especially efficient means of population control.

It is likely that abundance of young aelwives and subsequent recruitment were also affected by a more fundamental limiting factor than predation in Lake Michigan. Adults that produced the poor 1966 year-class were in poor condition near the population peak when zooplankton was depleted, whereas the adults that produced the numerous young-of-the-

year in 1968–70 were in excellent condition (Table 12). Nikolsky (1961) believed that by means of changes in abundance and quality of progeny produced, the stocks of spawners of some species adaptively react to changes in foraging conditions. He noted that high fluctuations in abundance are usually common among planktivorous fishes and that the qualitative characteristics (e.g., fat content) of the reproducitve products are important for suvirval during the mixed feeding stage when young must shift to external food.

Stock Size and Fishing Intensity

An estimated 490 million lb (222 million kg) of alewives were available to bottom trawls[2] during the extensive sampling by the *Kaho* in spring 1964, when most of the adult alewife population was located over depths of 50 fathoms and shallower (for depth distribution see Reigle 1969a, c). That alewives were heavily concentrated near bottom at the trawl locations in 1964 was indicated by some of the highest catch rates yet recorded in experimental fishing in southeastern Lake Michigan. Projection of the estimate of available fish into other years in proportion to the previous fall catch rates for experimental and commercial trawling gave 2.45 billion lb (1.11 billion kg) or 171 lb per surface acre (191 kg per hectare) of the entire lake near the population peak in spring 1967 (Table 16). The estimate of alewives available to trawls during experimental fishing by the *Kaho* and *Cisco* in spring 1969 (156 million lb; 70.7 kg) was only 47% of the value projected from the 1964 estimate (333 million lb; 151 million kg), suggesting that the population was less concentrated near the bottom in 1969. Even on the basis of the small 1969 estimate and the respective fall catch rates, 1.15 billion lb (0.52 billion kg) of alewives may have been available to trawls in spring 1967.

The dead alewives deposited on beaches during the 1967 summer die-off were also evidence of the large populations present in the mid-1960s. An average of 144 lb per foot of beach (range, 30–300 lb per ft) or 760,000 lb per mile (214,000 kg per km) were cleaned from beaches at Chicago, Ill., Kenosha and Racine, Wis., Traverse City, Mich., and four other locations (Greenwood 1970). If the average deposition rate for the entire lake was one-half the recorded rate, more than 300 million lb (139 million kg) of alewives were deposited. In addition, large quantities sank in the spring, summer, and preceding winter or deteriorated before they were removed.

Compared to the high natural mortality and the large changes in recruitment of various year-classes to bottom stocks, fishing mortality for alewives over the entire lake was relatively insignificant before 1969. The annual commercial catch through 1970

[2]N. J. Reigle (correspondence of March 23, 1966, on file at the Great Lakes Fishery Laboratory) calculated a standing crop much higher than this estimate. He arbitrarily doubled the weight of alewives available to trawls to compensate for avoidance, and further expanded the figure to include fish believed to be alewives located in midwater by echo sounder.

TABLE 16. Comparison between commercial production of alewives and alewives available to bottom trawls (*millons of pounds*) in Lake Michigan as projected from estimates of 490 and 156 million pounds in spring 1964 and 1969, respectively.

Year	Abundance index[a]	Commercial production	Available to trawls		Production as % of available fish
			Projected from 1964	Projected from 1969	
1963	100	5	605	284	0.8–1.8
1964	81	12	490[b]	231	2.4–5.2
1965	187	14	1131	530	1.2–2.8
1966	346	29	2093	983	1.4–3.0
1967	405	42	2450	1150	1.7–3.7
1968	175	27	1059	497	2.5–5.4
1969	55	29	333	156[b,c]	8.7–18.6
1970	99	33	599	281	5.5–11.7

[a]From the previous fall, see Table 14.

[b]The interval of one SE of estimate for 289 million lb of the 1964 estimate computed from 2 or more tows per section was 228–392 million lb; the interval for 113 million lb of the 1969 estimate was 81–163 million lb.

[c]Actual estimate of 126 million lb times 1.24 to adjust for greater area of lake fished in 1964 than in 1969.

was 18.6% or less of the estimated weight of alewives available to trawls, and therefore a smaller percentage of the total population (Table 16). Local effects of fishing were most likely the greatest in Green Bay, which produced more than half of the commercial catch, but the size of the annual migration which supported the summer poundnet fishery (peak near July 4) and trawl fishery in Green Bay is not known, nor is it known what fraction of the alewives in northern Lake Michigan spawn in Green Bay or how far they migrate. Effects of heavy local catches by trawling such as at Saugatuck could have been quickly compensated for by immigration from surrounding unfished areas.

In contrast to poundnets, which depend on the spawning migration, the Lake Michigan trawlers fished for alewives throughout the year except during adverse weather. Ice near shore also limited winter fishing in some years. A unit of trawling effort in May, when alewives were crowded inshore, produced more than double the weight produced by equal fishing effort in October or November, after postspawning dispersal (Fig. 7). Landings were therefore better than effort for indicating the seasonal distribution of fishing mortality generated by trawling.

The yield per recruitment to the trawl fishery for alewives in Lake Michigan is extremely low because of high natural mortality and the intrinsically low growth rate (Fig. 8). Almost 47% of the experimental catch in April 1968–70, for example, was composed of age-groups that were not yet available in maximum numbers to bottom trawls (Fig. 4). Although commercial production could be raised substantially by exploiting alewives over a greater area of the lake than at present, the yield per recruitment from any maximum fishing rate that might be sustained will be less than the initial weight of the recruitment. If total instantaneous mortality (Z), estimated as 1.5 (annual mortality 78%) in 1968–70, had a fishing mortality component of 0.5 (annual mortality 39%), undoubtedly much higher than the actual fishing mortality for southern Lake Michigan, each pound of alewives available in maximum numbers at age IV in fall would subsequently have yielded only 0.34 lb (0.15 kg) to the fishery.

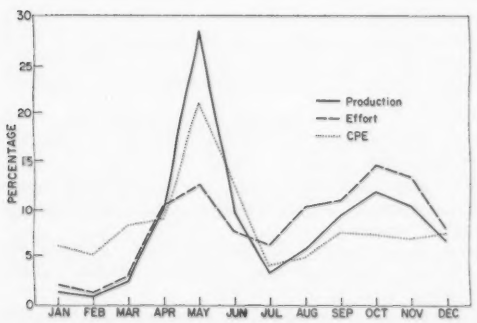

FIG. 7. Average monthly distribution of production (*lb landed*), effort (*hr fished*), and catch per unit of effort (*lb/hr*) in the trawl fishery of Michigan and Wisconsin waters of Lake Michigan, 1964–66.

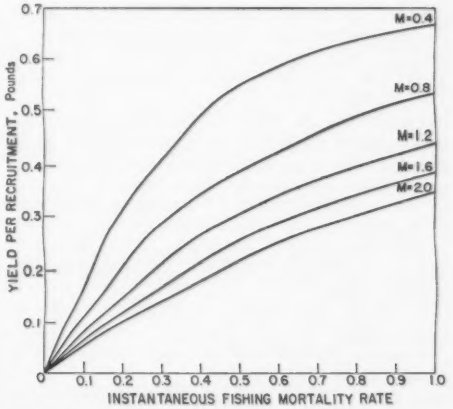

FIG. 8. Yield per recruitment to the trawl fishery for Lake Michigan alewives at different fishing mortalities and various natural mortalities (*M*) from 0.4 to 2.0. Calculated from maximum availability at age IV in fall through age VIII in spring, on the basis of growth after the 1967 die-off.

Future landings by the modest commercial fishery may be greatly affected by the forage requirements of the growing predator populations and the uncertain ability of the short-lived alewife to sustain heavy predation. It should be expected that the alewife population, which is so vulnerable to environmental effects, is in possible danger of collapse when subjected to an additional unrestrained limiting factor such as predation. This danger may be especially real in the relatively small confines of Lake Michigan.

Acknowledgments

L. Wells was mainly responsible for the continuity of many of the field investigations. Helpful suggestions were made by A. McLain and S. H. Smith. G. Sakagawa, J. Wilson, and A. Conedera read most of the scales, and P. Haack gave advice on parts of the statistical analyses. Various biologists of the Great Lakes Fishery Laboratory and of the Exploratory Fishing and Gear Research Base (directed by M. R. Greenwood) cooperated in the assessment surveys. The master of the R/V *Cisco*, R. Beauchamp, and of the R/V *Kaho*, J. Settersten and later C. Wilson, and crews of the two vessels contributed much to the success of the often difficult fall surveys.

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Tissue Culture Bioassay Method for Water Pollution with Special Reference to Mercuric Chloride[1]

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Li, M. F., and G. S. Traxler. 1972. Tissue culture bioassay method for water pollution with special reference to mercuric chloride. J. Fish. Res. Bd. Canada 29: 501–505.

The effect of $HgCl_2$ on multiplication and respiration of L-cells cultivated in suspension was studied. The nutritional history, growth phase, initial density of the cells, as well as the concentration of the serum supplement used in the test medium had significant effects on the sensitivity of the bioassay system. We concluded that the cells used for the test should be in the stationary phase at an initial cell density of approximately 2×10^5 per milliliter, and the test medium should be free of fetal calf serum.

Under our experimental conditions mercuric chloride at a concentration of 10 μg/liter or less inhibited the cellular multiplication significantly; the results indicated that this assay procedure could be adequate for monitoring water quality. The cellular respiration method, however, was less sensitive, but simple and rapid with results being made available within a few hours, and therefore useful for screening or preliminary testing of heavily polluted samples.

Li, M. F., and G. S. Traxler. 1972. Tissue culture bioassay method for water pollution with special reference to mercuric chloride. J. Fish. Res. Bd. Canada 29: 501–505.

Nous avons étudié l'effet de $HgCl_2$ sur la multiplication et la respiration des cellules-L cultivées en suspension. L'alimentation passée, la phase de croissance, la densité initiale des cellules, ainsi que la concentration du supplément sérique ajouté au milieu d'essai affectent nettement la sensitivité des essais biologiques. Nous en concluons que les cellules utilisées doivent être à la phase stationnaire et à une densité initiale d'environ 2×10^5 par ml, et que le milieu d'essai doit être libre de sérum de fétus de veau.

Dans nos expériences, le $HgCl_2$ à une teneur de 10 μg/litre ou moins a empêché de façon significative la multiplication cellulaire. D'après nos résultats, ce protocole d'essai biologique pourrait servir au contrôle continu de la qualité de l'eau. La méthode de respiration cellulaire, moins sensible, est néanmoins simple et rapide (les résultats en sont connus en moins de quelques heures) et est utile pour la mise de côté ou l'essai préliminaire d'échantillons fortement pollués.

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Industrial discharges and urban wastes have caused serious environmental problems; this is most noticeable in the effects on aquatic life. Fish exposure and oxygen residual tests have been suggested for monitoring water quality (Ballard and Oliff 1969). These methods are labor and time consuming and their sensitivity to pollutants varies with species, size, age, and physiological condition of the fish used (Lennon 1967). In recent years some chemical methods for determining pollutants have been advanced (Uthe et al. 1970). These, however, deal with only a particular pollutant, and cannot replace the bioassay method completely for overall water quality control. Thus a rapid and effective monitoring system is needed urgently for measuring the net deterioration in water quality.

Among the materials of immediate concern are mercury and its derivatives contributed to the environment from industrial effluents which cause serious pollution problems for aquatic animals (Bligh MS 1970). Accordingly, this study was performed to determine the effect of a representative mercuric compound, mercuric chloride, on cellular respiration and multiplication as well as the factors governing the sensitivity of this bioassay system.

Materials and Methods

Cell Culture and Growth Assay

Mouse cells (L-cells, clone 929) were cultivated in 50-ml spinner flasks, and the experimental system was essentially that described previously (Li and Jordan

[1]Presented in part at the Twentieth Annual Meeting of the Canadian Society of Microbiologists, June 2–5, 1970, at Dalhousie University, Halifax, N.S.

Printed in Canada (J2348)

1969; Li et al. 1970). The spinner modified Minimum Essential Medium[2] (MEM) was supplemented with 10% fetal calf serum (Medium A), 1% fetal calf serum, and 0.5% peptone (Medium B), or 0.5% peptone only (Medium C). The desired concentration of $HgCl_2$ solution was prepared in Hank's balanced salt solution (BSS), and added. The cells were enumerated using an electronic counter (Li and Stewart 1965).

Manometric Methods

The cell respiration studies were conducted using a Gilson Differential Respirometer[3] at 37 C. The BSS without carbonate, but buffered with tris-phosphate (monopotassium salt) (*p*H 7.1–7.2) and supplemented with essential amino acids and vitamins (Penso and Balducci 1963), was employed for preparing the cell suspension and the $HgCl_2$ solution. The cells were taken from stock cultures during the stationary phase, harvested by centrifugation at 500 × *g* for 5 min, washed by resuspension in the buffered BSS to about one-third of original volume, and centrifuged as before. The washed cells were resuspended to the desired cell concentration. A reasonable rate of respiration was obtained when 3×10^6 cells per Warburg flask were used. Conventional manometric techniques (Umbreit et al. 1964) were followed. The flask with cell suspensions and $HgCl_2$ solution or the buffered BSS as control were shaken at a rate of 94 strokes per minute for 30 min before the system was closed. The readings were taken at 1-hr intervals for 5 hr.

Results

Effect of Growth and Test Media on Cellular Sensitivity to $HgCl_2$

In our preliminary studies it was found that the presence of $HgCl_2$ in the spinner culture medium supplemented with 10% fetal calf serum (Medium A) markedly inhibited cellular multiplication. For the evaluation of the effect of the nutritional history of the cells, and the fetal calf serum concentration on the sensitivity of the growth assay system to $HgCl_2$ the cells were grown in both Medium A and Medium B. The cells were harvested at the same growth phase and tested in the two media containing 0.3 mg/liter of $HgCl_2$ (Fig.1). The greatest inhibition by $HgCl_2$ (0.3 mg/liter) was observed in the cells grown and tested in Medium B (Fig. 1A). When cells from the same stock culture (in Medium B) were tested in the medium containing 10% fetal calf serum (Medium A), the inhibitory effect of the $HgCl_2$ was reduced from 59 to 19% (Fig. 1B). However, when the cells grown in Medium A were tested using the same medium a 35% inhibition was observed (Fig. 1C). It is evident that both the nutritional history of the cells and the test medium are important factors in determining the sensitivity of the bioassay system. To evaluate the carry-over effect of fetal calf serum in the stock culture and its interference with $HgCl_2$, the medium in the stock culture (Medium B) was removed by low speed (500 × *g*) centrifugation and the cells were suspended in Medium C for inoculation. A parallel experiment was performed for comparison using the original stock culture for inoculation without removing the culture medium. Thus, the cells were tested in Medium B (with 1% fetal calf serum) or Medium C (with 0.3 mg/liter $HgCl_2$ or BSS as control) for 3 days. Results were:

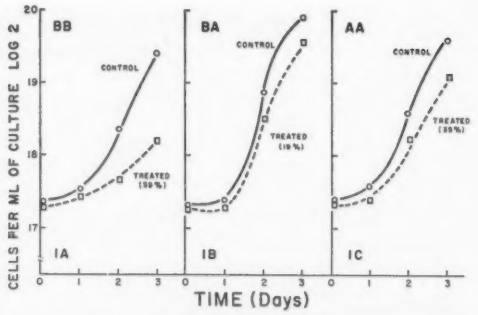

FIG. 1. Effect of growth and test media on the inhibition of cellular multiplication by $HgCl_2$ (3 mg/liter). BB, the cells grown and tested in Medium B; BA, the cells grown in Medium B and tested in Medium A; AA, the cells grown and tested in Medium A. The percentages (in parentheses) indicate the degree of inhibition.

Fetal calf serum concentration (%)	Percentage Inhibition: Inoculum centrifuged and suspended in Medium C	Percentage Inhibition: Inoculum not centrifuged (original stock medium)
1	65.8	47.4
0	100	100

The low speed centrifugation for removing the stock culture medium appeared to have little or no effect on the rate of cell multiplication during the 3-day experimental period. The removal of the stock culture medium from the inoculum appeared to effect a considerable increase in the sensitivity of the assay system.

[2]Becton, Dickinson, and Co., Canada Ltd., Clarkson, Ont.

[3]Gilson Medical Electronics, Middleton, Wis., USA.

Effect of Growth Phase of the Experimental Cells

A normal growth curve of the cells in the medium supplemented with 1% fetal calf serum and 0.5% peptone (Medium B) is shown in Fig. 2. After a short-lag phase the cells reached the logarithmic phase within 24 hr, which continued to 72 hr before reaching the stationary phase. From the culture the cells were harvested at 72 hr (Phase A) and 120 hr (Phase B) for testing against varying concentrations of $HgCl_2$ contained in Medium C (0.5% peptone); the results are shown in Fig. 3. The cells from the stationary phase (Phase B) were sensitive to the presence of $HgCl_2$ at concentrations of 1.0 to 2.5 μg/liter; in contrast, inoculum prepared from the actively growing phase (Phase A) appeared to be affected only slightly at or below concentrations of 10 μg/liter.

Since the initial cell density has also been noted to be an important factor for the sensitivity of the assay system (Li and Jordan 1969), the cells grown in Medium B, harvested during the stationary phase, and tested in fetal calf free medium (Medium C) at an initial cell density of approximately 2×10^5 per milliliter, were used throughout in our standard experiments.

Effects of $HgCl_2$ upon the Cellular Respiration

The respiration rates of cells grown in Medium A or B were measured manometrically (Fig. 4). In both media, oxygen uptake per unit of cells increased with the increase in cell density; the higher cell densities appeared to be associated with increased cellular activity. The cells grown in the medium containing lower levels of fetal calf serum (Medium

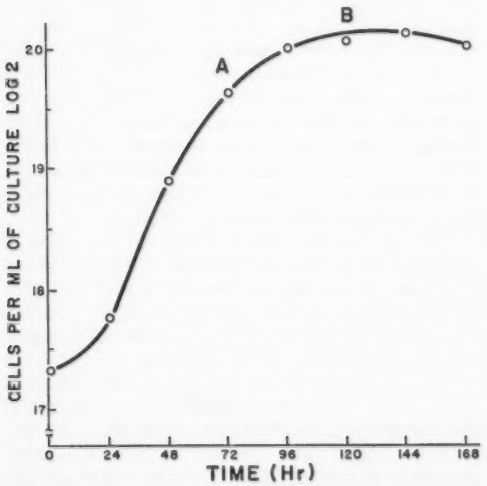

Fig. 2. Growth curve of the cells in Medium B at 37 C. A, cells sampled during actively growing phase; B, cells sampled during stationary phase.

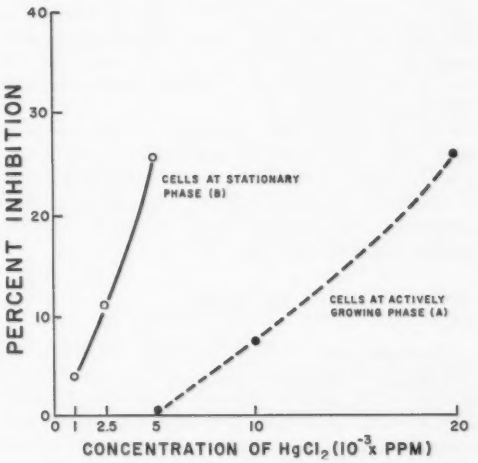

Fig. 3. Effect of $HgCl_2$ on inhibition of multiplication of cells tested at two different growth phases.

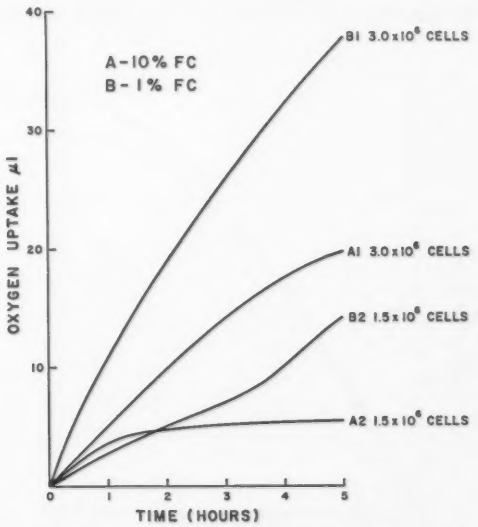

Fig. 4. Time course of oxygen uptake by two levels of cells grown in two different media. Cell A grown in Medium A; cell B grown in Medium B. Cells were incubated in the buffered and enriched balanced salt solution at 37 C.

B) consistently consumed more oxygen than those grown in the medium with 10% fetal calf serum (Medium A). Cells grown in Medium B with a density of approximately 3×10^6 per flask were used in the following experiments.

Figure 5 shows the inhibitory effect of $HgCl_2$ upon cellular respiration. The oxygen uptake by the cells was drastically reduced when $HgCl_2$ concentration was increased from 2 to 3 mg/liter. At the 4 mg/liter level the cellular respiration was essentially nonexistent.

To compare the effect of $HgCl_2$ on cellular respiration with that on cellular multiplication the results from a series of trials are summarized in Table 1. It is evident that the cellular multiplication measurement is far more sensitive to $HgCl_2$ than the cellular respiration assay.

TABLE 1. A comparison of the sensitivity to $HgCl_2$, of multiplication with respiration of spinner cells.

Concentration of $HgCl_2$ (*mg/liter*)	Percentage of Inhibition[a]	
	Cell respiration	Cell multiplication
5	100	100
3	86.2±19.8	100
1	5.2±4.7	100
0.1	0	100
0.05	0	100
0.02	0	79.4±25.3
0.01	0	43.8±18.8

[a]Mean ± standard deviation.

Discussion

The experiments indicate that both the nutritional history of the cells and the test medium are significant factors affecting the sensitivity of the bioassay system. Cells grown in low fetal calf serum concentration medium (Medium B) appeared to respond more to the high level of fetal calf serum in Medium A and to be less sensitive to $HgCl_2$ than cells grown in Medium A. This may indicate that cells adapted to the low fetal calf serum concentration medium (Medium B) have a different biosynthetic process from those maintained in Medium A. A study of the difference in metabolic process between the adapted and nonadapted cells would be of interest.

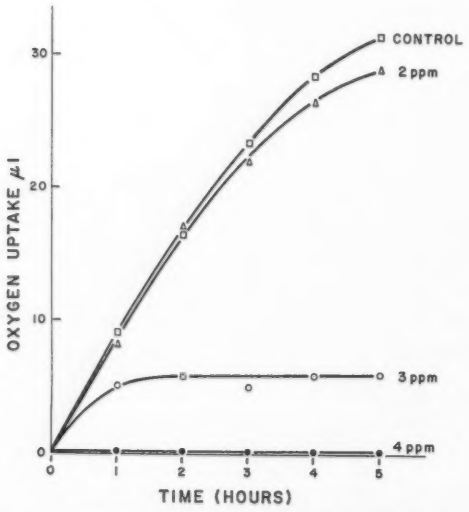

FIG. 5. Effect of $HgCl_2$ on the inhibition of oxygen uptake by the cells (3×10^6 cells per flask) grown in Medium B.

The importance of the fetal calf serum concentration for the sensitivity of the assay system is evident, since even a trace of the serum (0.1%), carried over from the original inoculum, resulted in significant reduction of the inhibitory effect of $HgCl_2$. The possible binding of the serum protein with $HgCl_2$ might make less Hg^{++} available or the bound mercury could be less toxic to the cell culture.

The phase of growth of the test cells plays an important role in the sensitivity of the assay system. Our limited data indicate that a choice of proper growth phase of the cells could improve the sensitivity of the assay system by a factor of 4 (Fig. 3).

The great difference in the sensitivity to $HgCl_2$ between cellular respiration and multiplication suggests that, in addition to its effect on the cellular enzyme systems (Brown and Edwards 1969; Kidby 1971), Hg^{++} may interact with cellular DNA, and thus inhibit cells at a particular stage of their division cycle (Matsuda and Takeuchi 1967).

Our cytological studies of the cells exposed to $HgCl_2$ indicated that cells exposed to $HgCl_2$ showed an enormous increase in size with a high incidence of multi-nuclei and an incompleteness of division. The cytopathic aspects of the cells exposed to $HgCl_2$ will be described in detail elsewhere.

The sensitivity of fish to $HgCl_2$ depends to a great extent on water temperature and the size of fish. In general, the developing eggs are more sensitive to $HgCl_2$ than the live animals. A concentration of 10 µg/liter of $HgCl_2$ in water will severely disturb the developing eggs of the sea urchin (*Paracentrotus lividis*), while a concentration of 5 µg/liter will retard egg development. A threshold for harm-

ful effects of $HgCl_2$ on the developing eggs is between 2–3 μg/liter (Wilber 1969). This level is far beyond the sensitivity of other proposed biological monitoring systems for water quality (Ballard and Oliff 1969). If the factors described in this paper, however, are carefully controlled the cell multiplication method of the spinner cells could be adequate for monitoring water quality. Although the cellular respiration method is less sensitive, it is simple and rapid and could be used for screening or preliminary testing of heavily polluted samples.

Acknowledgments

We thank Dr J. E. Stewart for his interest and assistance, and Dr M. S. Mounib for his review of the manuscript and constructive suggestions.

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Distribution of Herring (*Clupea harengus*) Larvae Along the Southern Coast of Nova Scotia with Observations on Their Growth and Condition Factor[1]

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SAMEOTO, D. D. 1972. Distribution of herring (*Clupea harengus*) larvae along the southern coast of Nova Scotia with observations on their growth and condition factor. J. Fish. Res. Bd. Canada 29: 507–515.

The distribution and abundance of herring larvae on the southern coast of Nova Scotia suggested the presence of a fall spawning population. Larvae were found in St. Margaret's Bay from late September to June. They showed a slower growth rate than larvae from the Clyde Sea, Scotland, and weighed less at a particular length than did larvae from the Clyde Sea and Boothbay, Maine. The larvae had a lower condition factor at 25 mm length than larvae from the North and Baltic Seas. No larvae were found on the Scotian Shelf during late May and early June, 1969, but were abundant during September and October. Herring spawning beds were reported from areas along the entire coast of Nova Scotia from Canso to Cape Sable.

SAMEOTO, D. D. 1972. Distribution of herring (*Clupea harengus*) larvae along the southern coast of Nova Scotia with observations on their growth and condition factor. J. Fish. Res. Bd. Canada 29: 507–515.

La distribution et l'abondance des larves de hareng au large de la côte méridionale de la Nouvelle-Ecosse suggèrent la présence d'une population qui fraye à l'automne. Nous avons capturé des larves dans la baie Sainte-Marguerite à partir de la fin de septembre jusqu'en juin. Ces larves croissent plus lentement que celles du Firth of Clyde, Ecosse. Pour une longueur donnée, elles pèsent moins que celles du Firth of Clyde et de Boothbay, Maine. A une longueur de 25 mm, les larves ont un indice d'embonpoint plus faible que celui des larves des mers du Nord et Baltique. Nous n'avons pas trouvé de larves sur le plateau néo-écossais à la fin de mai ou au début de juin 1969. Par contre, elles étaient abondantes en septembre et octobre. On a signalé des frayères de hareng tout le long de la côte de la Nouvelle-Ecosse, depuis Canso jusqu'au cap de Sable.

Received November 24, 1971

LEIM (1957) and Tibbo (1957) stated that the herring spawned during the summer months in the area of Nova Scotia west of Halifax and that this population consisted of large old herring. Vertebral count analysis suggested that the herring were of single and homogeneous population. Leim (1957) believed that spawning in the area east of Halifax was similar to that found for the herring in the Gulf of St. Lawrence, where there are two spawning seasons, a major one in May or early June and a smaller one in September. These are the only published works on the spawning of herring on the east coast of Nova Scotia.

The condition factor of herring larvae has been used as an indicator of high or low potential larval mortality (Chenoweth 1970). Vilela and Zijlstra (1971) believed the condition of herring larvae in the North Sea was determined by the availability of food and temperature, and that the condition of the larvae determined larval mortality. The lower the condition factor presumably the higher will be the mortality. Shelbourne (1957) showed a correlation between the condition factor of plaice larvae and the availability of food. In a study of the condition factor of Clyde Sea herring larvae and the biomass of planktonic food, Blaxter (1971) found a negative correlation between the two, and that years with the lowest condition factor showed the lowest subsequent brood strength of herring.

This study was designed to gather further data from the eastern coast of Nova Scotia on the spawning areas of herring (*Clupea harengus*), the time of spawning and the abundance of herring larvae at different times of the year. Data on the

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biomass of copepods were collected to determine if a relation existed between the numbers of larvae and the biomass. A comparison of the numbers of larvae caught using two different types of sampling gear and the numbers caught during day and night was made.

The condition factor and growth rate of herring larvae during the fall and winter were studied and compared to that of herring larvae from the coast of Maine, and from parts of the North, Baltic, and Clyde Seas, to determine if the environment on the coast of Nova Scotia was as favorable to the larvae as those mentioned above.

Methods

Sampling Gear

Herring larvae and zooplankton samples were taken with a modified Icelandic highspeed plankton sampler (Sameoto MS 1971) with a filtering efficiency of 100% (Kawerninski 1968). Samples were also taken with a 6-ft Isaacs-Kidd midwater trawl with a 6-mm mesh liner.

Field Survey Design

Horizontal high-speed samples were made along six transects within St. Margaret's Bay and along two transects outside the Bay each 1.5 nautical miles long. Each sample filtered 55 m^3 of water. Samples were taken simultaneously at depths of 2, 18, and 36 m at a speed of 4 knots. Sampling was carried out at 1 month intervals, weather permitting, from October 1967 to May 1970.

Isaacs-Kidd trawl samples were taken at depths of 18 and 36 m at a speed of 4 knots, over transects 3 nautical miles long. Five transects were sampled within the Bay and two outside the Bay in the same regions that were sampled by the highspeed samplers. Sampling with the trawl was done at the same time of month as the high-speed sampling, but only from December 1967 to February 1969.

Day and night samples were taken with the high-speed sampler from October 1967 to June 1968, after which time only night time samples were taken. All Isaacs-Kidd trawl samples were made after dark.

Scotian Shelf sampling was carried out during two cruises in 1969. In the spring (May 27–June 5) samples were taken at depths of 10 and 27 m at 67 stations, those in the fall (September 29–October 9) at 10, 27, and 54 m at 121 stations. In both cruises samples were taken only with the modified high-speed sampler by day and night. Towing was at a speed of 4 knots on successive transects one nautical mile long. Each sample filtered 36 m^3 of water. All depths were sampled simultaneously.

Sample Treatment

Zooplankton samples were preserved in a 5% buffered formalin and seawater solution. Herring larvae from the samples were counted, measured, and weighed after blotting on filter paper. Standard and total lengths of the herring larvae were measured to the nearest millimeter after the animals had been preserved for about 1 month. Dry weight determinations of the preserved larvae followed drying at 60 C for 48 hr.

The relation between standard length and total length of the larvae determined by measuring both lengths for 25 larvae was:

$$\text{Standard length} = 1.97 + 0.86 \text{ Total length}$$

The percentage weight loss of the larvae due to preservation for 1 month, determined by weighing 20 animals 1 day after preservation then reweighing 30 days later, was $3.8 \pm 3.4\%$.

The condition factor of the larvae was calculated from the following formula (Hempel and Blaxter 1961):

$$\text{Condition Factor} = \frac{\text{dry weight } (mg) \times 1000}{\text{standard length } (mm)^3}.$$

Species of zooplankton other than copepods were removed from the sample. Water was removed from the copepod sample by vacuuming it over a 30 μ filter until water ceased to drip for 30 sec. The sample was then weighed.

Statistical Methods

The mean values for numbers of larvae and weights of copepods are arithmetic means. The variation about the means is expressed as the logarithmic coefficient of variation ($V = \text{antilog}_{10} S_T - 1$) (Cassie 1968), where S_T is the standard deviation calculated from the logarithms of the raw data.

Results

St. Margaret's Bay

Young herring larvae still in the yolk sac stage were found in St. Margaret's Bay only during the fall, and first appeared in samples on September 16, 1969. Figure 1 gives the densities of herring larvae in the Bay as estimated by sampling with the high-speed sampler.

The relative copepod biomass like the herring density was much higher in October 1968 than in October 1969 (Fig. 2). The high-speed sampler data showed a decline in density of larvae through the fall and winter, while the numbers from the Isaacs-Kidd midwater trawl samples (Table 1) remain approximately the same.

The number of larvae caught per unit volume of water showed a rapid decline from October to December in all years covered by this study (Fig. 2). This decline occurred when the larvae were between 8 and 17 mm long, but may have started with animals smaller than 8 mm. Insufficient data

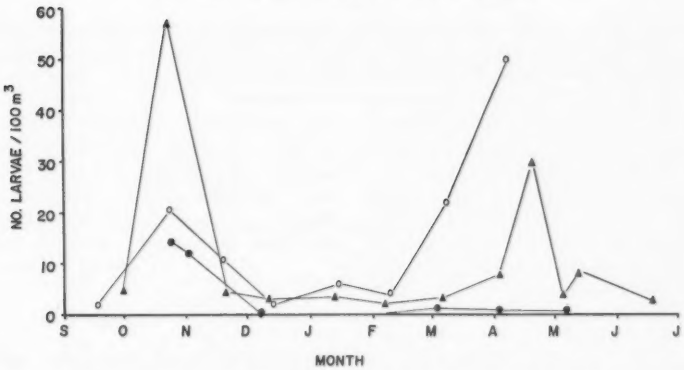

FIG. 1. Number of herring larvae per 100 m³ of water in St. Margaret's Bay during the fall to spring period. (● 1967, day samples; ▲ 1968, night samples; ○ 1969, night samples).

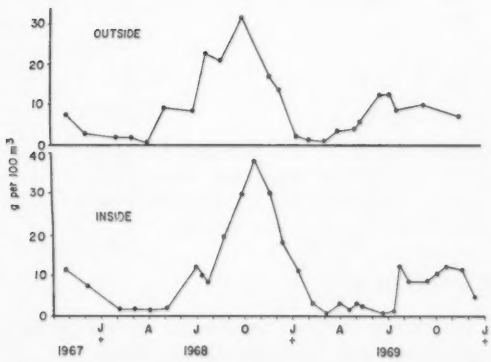

FIG. 2. Biomass changes of copepods with time inside and outside St. Margaret's Bay.

are available for this size range. In 1968 and 1969, the density remained relatively constant after November until about March or April, at that time there was an increase apparently due to an influx of larvae from outside the Bay. The spring increase in larval abundance did not appear for the larvae hatched in the fall of 1967, possibly because samples were taken during the day. No evidence was found for a regular spring or early summer spawning stock. A few larvae in the yolk sac stage were collected in the Bay in June 1968, but they were very scarce and were only collected during one sampling period.

Curves showing the growth rate of herring larvae from late fall to spring and the mean temperature for St. Margaret's Bay for this period are given in Fig. 3. A parabola fitted to body length and age data gave the equation:

$$\text{body length} = 6.1 + 0.2\,x - 0.0003\,x^2$$

where: x = age in days.

A similar parabola was fitted to length–age data for formalin preserved herring larvae from the Clyde Sea area of Scotland taken from Marshall et al. (1938) (Fig. 3).
The equation for these data was:

$$\text{body length} = 0.51 + 0.55\,x - 0.001\,x^2$$

There was no significant difference between the regression lines for the relation between total body length and the oven dry body weight of the herring larvae collected on different dates in the Bay during 1970. Therefore, the data for February, March, and May were combined to give one regression line (Fig. 4) with the equation:

$$\text{Weight} = \text{Length}^{4.49}$$

For a given length the St. Margaret's Bay herring weighed less than those of Boothbay Maine and the Clyde Sea herring (Fig. 4). Only a small part of this difference can be attributed to effect of longer storage time in the formalin solution.

The condition factor for individual larvae taken in February, March, and May, 1970 are shown on Fig. 5. The regression equations for the condition factors (y) versus the body length in millimeters (x), the 95% confidence limits for the slopes, and r^2 for each month's larvae were:

	Regression equation	95% CL	r^2
Feb.	$y = 0.00097\,x^{1.67}$	1.06 and 2.27	0.74
Mar.	$y = 0.0188\,x^{0.79}$	0.16 and 1.41	0.34
May	$y = 0.000074\,x^{2.40}$	1.94 and 2.86	0.82

TABLE 1. Mean number and coefficient of variation (V) of herring larvae caught per 100 m³ at night in the 6-ft Isaacs-Kidd midwater trawl (IK) and the highspeed sampler (IHSS) inside and outside St. Margaret's Bay.

	Inside				Outside			
	IHSS		IK		IHSS		IK	
Date	$\bar{X}$	V	$\bar{X}$	V	$\bar{X}$	V	$\bar{X}$	V
1967								
Dec. 6–7	0		0.3	2.8	–		0.07	
1968								
Feb. 5–7	0		0.1		0.8	0.4	0.6	0.3
Mar. 3	0.5	0.06	0.2	1.6	–		0.1	
Apr. 2–3	–		1.6	8.1	29.0	5.1	8.2	0.3
May 6	–		0.2	2.6	–		1.4	11.9
Sep. 27–30	4.5	1.0	0.04	0.8	40.0	4.7	0.2	0.1
Oct. 21–23	57.0	7.0	1.2	1.2	–		0.2	0.1
Nov. 20–21	4.5	0.4	0.3	1.4				
Dec. 11–12	2.9	0.3	0.2	0.6				
1969								
Feb. 6	2.0	1.4	0.2	0.9	1.0	1.9	1.2	2.0

r^2 is percentage of the variance explained by the regression.

There was no significant change in the relation between condition factor and body length over the period covered by the samples. Insufficient data were available to place any significance in the higher condition factor for the larvae between 20 and 25 mm in the March sample.

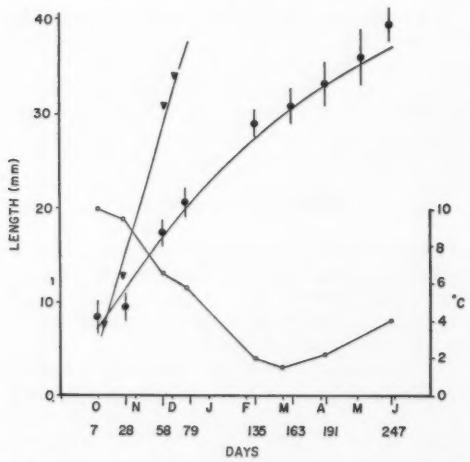

FIG. 3. Growth of herring larvae in St. Margaret's Bay throughout the winter compared to the growth of herring larvae in the Clyde Sea, Scotland. (● are mean values; the vertical bars represent one standard deviation; ▼ values from Marshall et al. 1938, for Clyde Sea herring; ○ mean water temperature for St. Margaret's Bay).

SCOTIAN SHELF

No herring larvae were collected on any of the sampling stations during the spring cruise.

The biomass of copepods during the spring cruise did not differ significantly between the day and night samples, but a greater biomass was found at 10 m than at 27 m (Table 2). The average biomass of copepods for the two depths on the different stations is shown in Fig. 6. Contours following a biomass of 10 and 20 g/100 m³ showed an area of high copepod density on the western tip of Nova Scotia, while a low biomass was found along the edge of the shelf and over the shallows near Sable Island.

In the fall cruise of 1969, herring larvae between 7 and 12 mm length and beyond the yolk sac stage were found along the entire coast of Nova Scotia, with concentrations at the mouth of Chedabucto Bay and over Canso Bank (Fig. 7).

Herring larvae occurred in 15 samples from a depth of 10 m, 15 samples from 27 m, and 10 samples from 54 m. It is noteworthy that, at the respective depths only 1, 3, and 3 samples were taken during daylight hours.

During the fall cruise the biomass of copepods was significantly greater (t = 6.25, df = 117; P = 0.05) for the night samples than for the day samples for all depths.

Areas of low copepods biomass were found over the Sable Island shallows and along the edge of the Shelf (Fig. 8). No areas of high copepod biomass were found as in the spring. No significant correlation was found between the biomass of copepods along the coast and the presence or estimated abundance of herring larvae.

Discussion

This study has shown that the Atlantic herring spawns along most of the southern coast of Nova Scotia, and that during the period 1967–69 the herring larvae in St. Margaret's Bay hatched by late September and early October and remained in the region until the following summer.

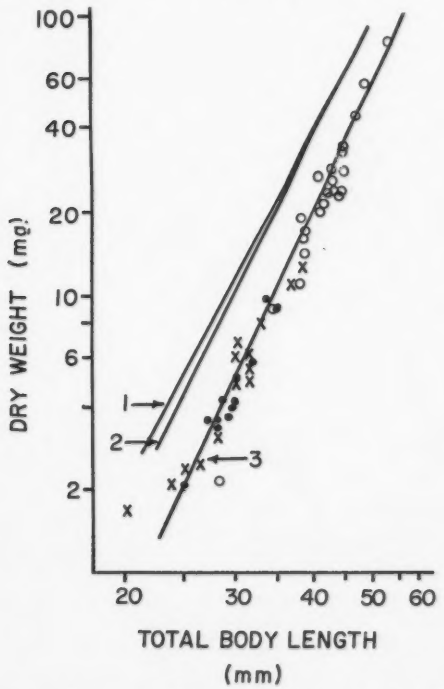

FIG. 4. Regressions for total body length and dry formalin weight of herring larvae from: 1. Boothbay, Maine (Chenoweth 1970; Chenoweth's data were converted to total lengths by the regression equation in the Methods), 2. Clyde Sea (Marshall et al. 1938); 3. St. Margaret's Bay (sampling dates: ● February 9; × March 7; ○ May 26 1970).

No herring larvae were found at any of the sampling stations on the Scotian Shelf during the spring cruise, but larvae were abundant at most stations along the coast during the fall cruise. These findings indicated that the herring spawned along the entire coast of the study area and had it been possible to sample only at night it is likely larvae would have been found at all inshore stations. This is supported by Sameoto (1971) who stated that interviews with fishermen along the coast indicated that fall spawning beds were found in areas along the entire coast studied.

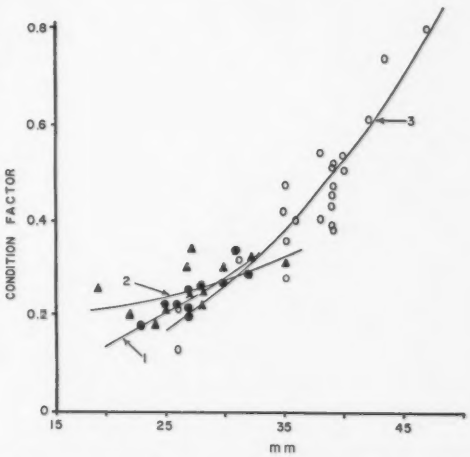

FIG. 5. Relation between condition factor and standard body length for herring larvae in St. Margaret's Bay. Regression lines are: 1. for larvae collected on February 9 (▲); 2. collected March 7 (●); 3. collected May 26, 1970 (○).

TABLE 2. Biomass of copepods as gram wet formalin weight/100 m³ of water on the Scotian Shelf.

Depth (m)	Day		Night	
	Spring			
	$\bar{X}$	V	$\bar{X}$	V
10	14.1	1.7	16.0	0.9
27	11.8	0.7	10.0	0.6
mean	12.9	0.8	13.0	0.6
	Fall			
10	3.6	1.4	9.5	1.6
27	5.8	1.4	10.4	1.5
54	5.8	1.8	8.8	0.8
mean	4.9	0.9	9.7	1.1

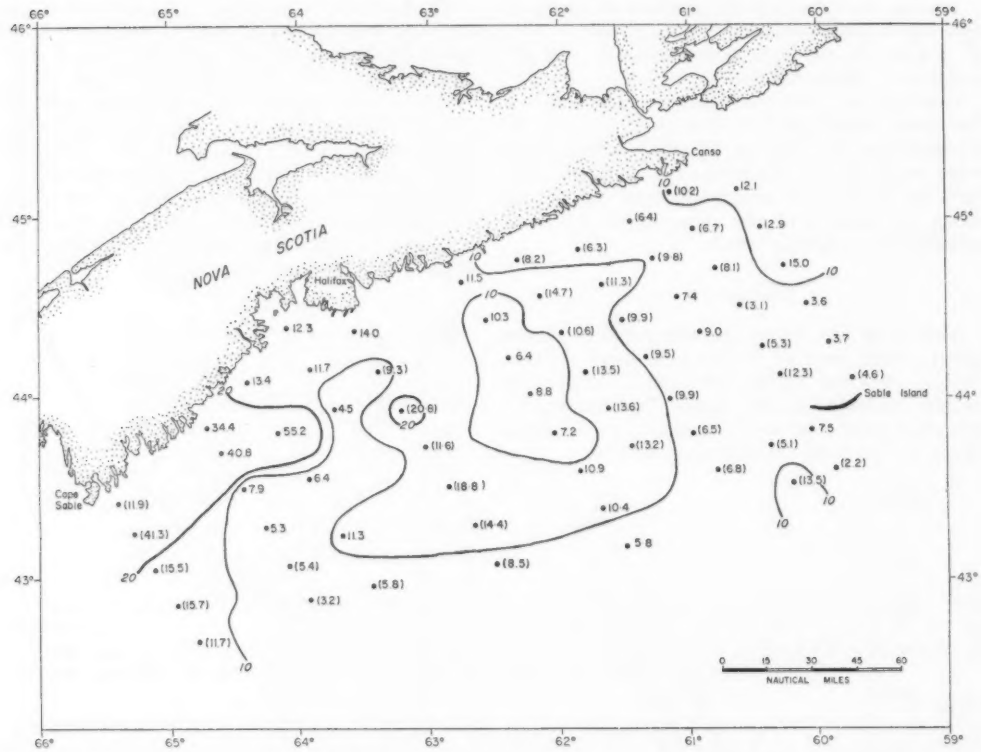

FIG. 6. Average biomass of copepods as g/100 m³ at 10 and 27 m depth found during the spring cruise. Contour lines represent areas having a biomass of 10 and 20 g of copepods (wet wt). Bracketed numbers represent night samples.

No evidence was found to suggest that herring spawning grounds occurred on the Scotian Shelf at any great distance from the coast. Herring larvae were found on the Shelf, but it is not known whether these larvae were carried there by currents from the inshore regions or whether they originated from spawning beds on the Shelf itself. The concentration of larvae found over the area of Canso Bank may have come from within Chedabucto Bay. Forrester (1971) found that water from within the Bay was carried out over the Bank in the late winter months, and it is highly probable that the same current pattern exists in the fall. If there are spawning areas on the Shelf, they are relatively unimportant compared to the inshore regions as shown by the distribution and numbers of larvae.

The apparent scarcity of spring spawning along the coast is puzzling, because spring spawning herring are reported from Chedabucto Bay and the Bras d'Or Lakes of Cape Breton (Sameoto MS 1971). Factors other than temperature must be involved as no significant temperature difference exists between the water temperature of Chedabucto Bay and coastal Nova Scotia (H. J. A. Neu personal communication).

The night samples caught larger numbers of larvae than those taken during hours of light. This was most obvious during the fall cruise on the Scotian Shelf. Wood (1971) found herring larvae near the seabed during the day, but at night the vertical distribution was close to being random. To obtain a truer picture of the larval population in a region it is obviously very important to sample during the hours of darkness.

The decline in larval numbers in October and November in St. Margaret's Bay may have resulted from them being flushed out of the Bay. Sharaf El Din et al. (MS 1970) showed that the upper 10 m in St. Margaret's Bay had a flushing time of 10 days. Predation may have also been important

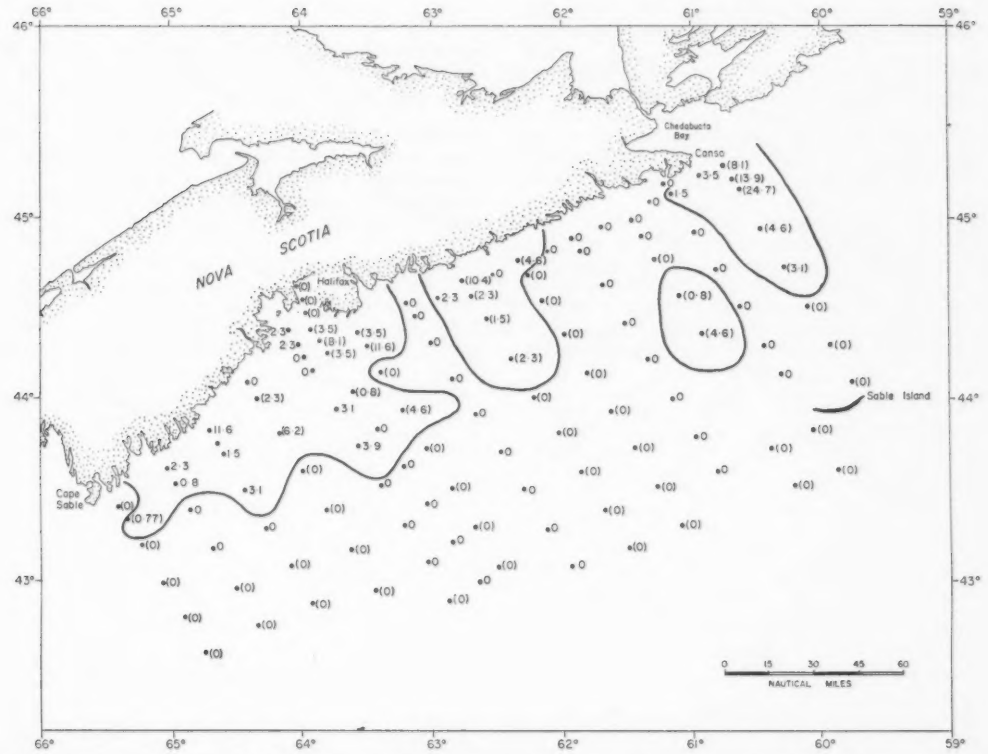

FIG. 7. Average number of herring larvae per 100 m³ at 10, 27, and 54 m depth during the fall cruise. Contour line represents estimated area containing at least 0.5 larvae per 100 m³. Bracketed numbers represent night samples.

in reducing the larval population. A large population of the chaetognath *Sagitta elegans* is present in the Bay at the time of the fall spawning (Sameoto 1972), and these may take a heavy toll on young stage larvae.

The increase in numbers of larvae about 30 mm length in St. Margaret's Bay during April 1969, and March and April 1970, indicated that larvae come into the Bay in the late winter and early spring with water masses from some other area along the coast. The general flow of the currents is from the Canso region toward Cape Sable, therefore, these larvae may have originated from a coastal area east of St. Margaret's Bay. Graham and Davis (1971) found a similar increase in herring larvae during March and April on the coast of Maine. They attributed this increase to inshore migrations of larvae from regions beyond the headlands of the estuary in which they were sampling.

The condition factor for larvae 20 mm long was between 0.15 and 0.2 which was very close to that given by Hempel and Blaxter (1961) for herring larvae of the same size taken from the Downs and Bank regions of the North Sea and the Baltic. But the 25 mm larvae in St. Margaret's Bay had a poorer condition than those from the above two regions. The Downs' herring condition was about 0.3 and that of the Baltic herring about 0.4, while the St. Margaret's Bay herring condition was approximately 0.2.

The rate of growth of Clyde Sea herring larvae was more than twice that of the St. Margaret's Bay larvae. The mean water temperature during the first $2\frac{1}{2}$ months of growth was 8 C for the St. Margaret's Bay population and 7 C for the Clyde Sea population (Marshall and Orr 1927). Therefore, the differences in the growth rates during this period must be due to factors other than temperature. Temperature may be important during winter and spring in the Bay, for from February to April the mean temperature is about 2 C. In addition to the low water temperature, the biomass of the

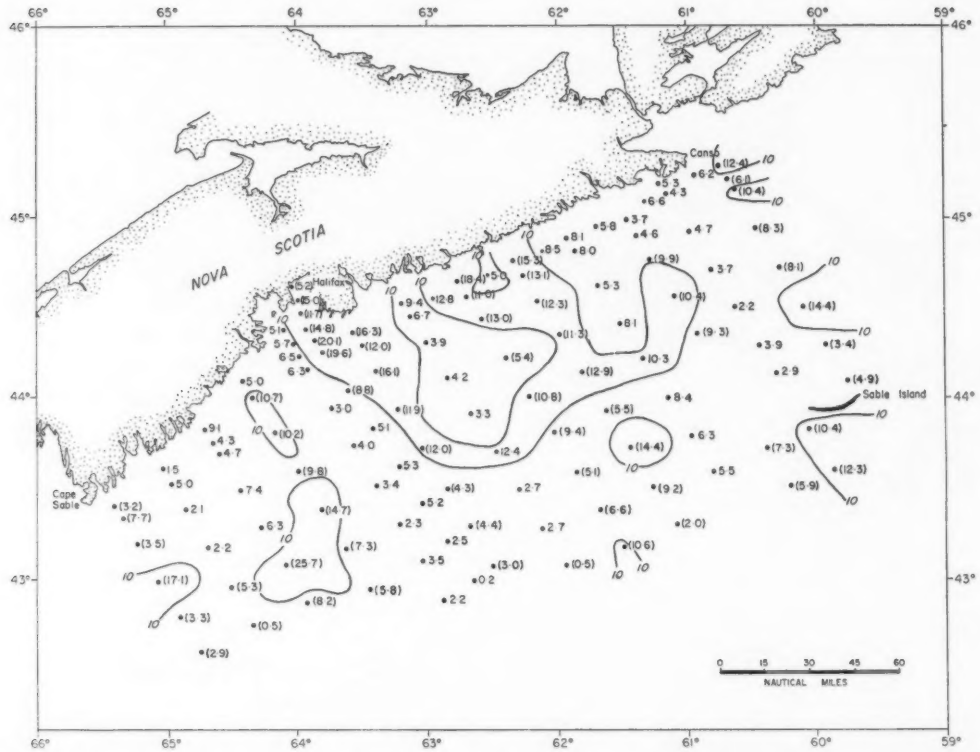

FIG. 8. Average biomass of copepods as g/100 m³ at 10, 27, and 54 m found during the fall cruise. Contour line represents area having a biomass of 10 g of copepods (wet wt). Bracketed numbers represent night samples.

copepods, on which the herring larvae feed, is at its lowest level at this time of year. But the herring larvae continued to grow at a uniform rate throughout the winter. This suggests that enough food was present to maintain growth but not enough to produce a condition factor as high as that of larvae from the other regions mentioned above.

Acknowledgments

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Croissance en longueur et en poids des perchaudes *Perca flavescens* de la Grande Anse de l'île Perrot au lac Saint-Louis

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FORTIN, R., et E. MAGNIN. 1972. Croissance en longueur et en poids des perchaudes *Perca flavescens* de la Grande Anse de l'île Perrot au lac Saint-Louis. J. Fish. Res. Bd. Canada 29: 517–523.

La détermination de l'âge des perchaudes a été faite à partir des os operculaires de 2170 spéciemens capturés tout au long de l'année, de juin 1967 à octobre 1969. Il a fallu tenir compte, dans les rétrocalculs, d'une allométrie de croissance de l'os operculaire. La croissance des perchaudes de la Grande Anse est excellente. Les mâles grandissent plus lentement que les femelles. La croissance saisonnière débute en mai et se termine en septembre. Les poissons à croissance rapide atteignent la maturité sexuelle à un plus jeune âge que ceux à croissance lente. L'exposant de la relation longueur–poids est 3.107. C'est en hiver que les perchaudes femelles de la Grande Anse ont l'indice d'embonpoint le plus fort, cela à cause du poids élevé des glandes génitales.

FORTIN, R., et E. MAGNIN. 1972. Croissance en longueur et en poids des perchaudes *Perca flavescens* de la Grande Anse de l'île Perrot au lac Saint-Louis. J. Fish. Res. Bd. Canada 29: 517–523.

In this study, growth in length is based upon age determination on the opercular bones of 2170 specimens, collected throughout the year from June 1967 to October 1969. The opercular bone shows allometric growth and this is taken into account in back calculations. Grande Anse perch show comparatively rapid growth. Growth of males is slower than that of females. Seasonal growth extends from May to September. Faster growing fish reach sexual maturity earlier in life. Length–weight relationship exponent is 3.107. Due to the weight of the gonads, female perch show maximum condition index values in winter.

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LE lac Saint-Louis, situé à proximité de Montréal, est actuellement l'objet de plusieurs études écologiques, dont le but très général est l'estimation de la production de matière vivante aux différents niveaux trophiques. La perchaude *Perca flavescens* est abondante dans ce lac et elle constitue une étape importante dans l'utilisation et la transformation de l'énergie dans ce système. C'est pourquoi nous nous sommes intéressés à la croissance de ce poisson.

Matériel et Méthodes

Les spécimens ont été capturés dans la Grande Anse, située dans la section nord-ouest du lac Saint-Louis (Magnin 1970). Les captures ont été bimensuelles de juin à octobre 1967 et mensuelles de novembre 1967 à octobre 1970. Les appareils de pêche utilisés incluaient des seines, des filets maillants (1½, 2 et 2½ po. maille étirée), et des filets-trappes. Après chaque pêche, nous avons relevé la longueur totale, le poids, le sexe, l'état de maturité, et le poids des gonades des poissons capturés, et nous avons recueilli sur chacun des écailles et l'os operculaire gauche.

Pour la lecture de l'âge, nous avons finalement préféré l'os operculaire aux écailles pour les mêmes raisons que LeCren (1947) et Bardach (1955). Pour l'étude de la relation existant entre la longueur totale du poisson (LT) et la longueur de l'os operculaire (Lop) et aussi pour le rétrocalcul de la croissance, nous avons utilisé la même méthode que LeCren (1947); comme ce dernier, nous avons observé une allométrie de croissance entre LT et Lop et nous avons utilisé, pour le rétrocalcul, la formule:

$$LT_x = \frac{LT_y \cdot Lop_x^b}{Lop_y^b}$$

dans laquelle on reconnaît les longueurs totales et les longueurs de l'os operculaire aux moments de la formation des annuli (x) et de la capture (y); dans le cas de LeCren (1947), b (0.920) était la pente de la droite $Y = a + bX$, où $Y = \log LT$ et $X = \log Lop$; dans notre cas, b (0.908) est la pente de l'axe majeur logarith-

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mique de LT en fonction de Lop (Jolicoeur et Mosimann 1968).

La croissance des perchaudes sera illustrée à l'aide des longueurs totales moyennes rétrocalculées lors de la formation du dernier annulus. Nous avons exprimé mathématiquement cette croissance à l'aide du modèle de von Bertalanffy, en appliquant la méthode de calcul de Tomlinson et Abramson (1961) à nos données.

Résultats

Croissance en longueur au cours d'un cycle vital

La figure 1 donne un aperçu des données âge-longueur obtenues; les spécimens de 11 ans et plus sont peu nombreux dans notre échantillonnage, et ils n'ont pas été inclus dans le calcul du taux de croissance; il faut cependant mentionner que le plus vieux spécimen mâle avait 15 ans et le plus vieux spécimen femelle, 13 ans. Par contre, le plus long mâle mesurait 275 mm et la plus longue femelle, 317 mm.

La figure 2 montre que, dès l'âge de 2 ans et parfois dès l'âge d'un an, les mâles diffèrent statistiquement des femelles par leur longueur moyenne et par leur accroissement annuel moyen; à partir de 7 ans, cependant, et parfois dès l'âge de 5 ans, les accroissements annuels moyens ne diffèrent plus statistiquement, mais les longueurs demeurent significativement différentes; l'écart qui s'est établi entre les deux sexes au cours des premières années se maintient au cours des années suivantes. Notons aussi que le plus fort écart séparant les accroissements annuels des mâles et des femelles est observé durant la troisième année, alors que les mâles sont adultes et que les femelles ne le sont pas. La figure 3 illustre les longueurs moyennes rétrocalculées lors de la formation du dernier annulus et les équations de von Bertalanffy pour les mâles:

$$L_t = 258.645\ [1 - e^{-0.290(t+0.126)}]$$

et pour les femelles:

$$L_t = 290.301\ [1 - e^{-0.291(t-0.037)}]$$

Les mâles mesurent 73, 153, 201, 223, 236 mm à 1, 3, 5, 7, et 9 ans; aux mêmes âges, les femelles mesurent 74, 168, 222, 253, et 267 mm.

En comparant statistiquement les longueurs totales moyennes d'individus femelles adultes et juvéniles de même classe d'âge (tableau 1), nous avons constaté qu'à un âge donné, les femelles adultes sont plus longues que les juvéniles.

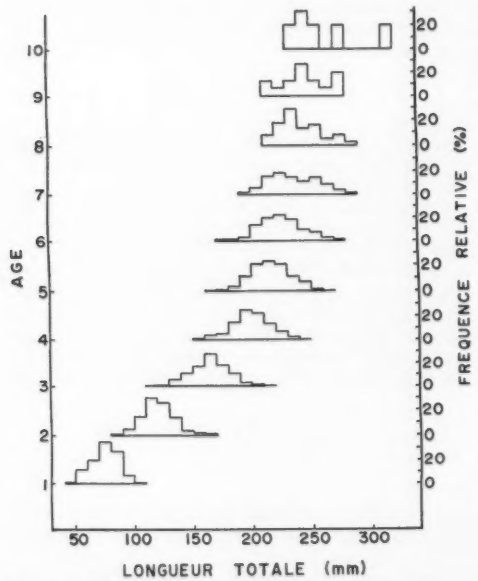

FIG. 1. Histogramme de fréquence des tailles des perchaudes aux différents âges.

Croissance en longueur au cours d'un cycle saisonnier

Le tableau 2 donne les accroissements saisonniers moyens obtenus par rétrocalcul; la croissance saisonnière moyenne, pour l'ensemble des poissons capturés de juin 1967 à avril 1969, est illustrée à la figure 4; auparavant, nous avions exprimé la croissance saisonnière en pourcentage de la croissance annuelle totale, mesurée chez des poissons de même classe d'âge, capturés au cours des années subséquentes (Hile 1941). Les perchaudes de la Grande Anse réalisent 10% de leur croissance en mai, 30% en juin, 65% en juillet, 90% en août, et 100% en septembre. En admettant que la saison de croissance est pratiquement terminée lorsque 90% de l'accroissement annuel est atteint (Gerking 1966), nous pouvons dire que la période de croissance de ces poissons dure quatre mois, soit du début du mois de mai au début du mois de septembre.

Relation longueur–poids et croissance en poids

Le tableau 3 montre que les femelles deviennent plus lourdes que les mâles à mesure que la longueur augmente; en appliquant la méthode des moindres carrés aux logarithmes des données longueur–poids de ce tableau, nous avons établi une équation pour les mâles:

$$\log P = -5.105 + 3.083 \log LT$$

et une pour les femelles:

$$\log P = -5.161 + 3.113 \log LT$$

Les courbes de croissance en longueur des mâles et des femelles ont été converties en courbes de croissance en poids (Fig. 3) à l'aide de ces deux équations; les mâles pèsent 4, 44, 98, 143 et 173 g à 1, 3, 5, 7, et 9 ans; aux mêmes âges, les femelles pèsent 4, 58, 139, 206 et 253 g.

Rapport gonosomatique et condition

Les variations saisonnières du rapport gonosomatique sont présentées à la figure 5; les moyennes mensuelles correspondent au rapport gonosomatique d'un individu de longueur moyenne. A cause des faibles effectifs mensuels, nous n'avons calculé qu'un rapport gonosomatique moyen annuel pour les mâles juvéniles, soit 0.14% du poids corporel. Chez les femelles juvéniles, le rapport gonosomatique

♂

Groupe d'âge	ANNULUS 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	N
1	73 73															90
2	68 68	116** 48**														127
3	66** 66**	116** 49**	152** 36**													75
4	72 72	123** 51**	160** 36**	184** 23												71
5	67 67	120 53	162** 42**	187** 25**	201** 13**											132
6	68 68	118** 51**	161** 43**	188** 27**	204** 16**	215** 11**										145
7	66 66	115** 49**	158** 43**	187** 29**	205** 17**	215** 11**	223** 9									79
8	71 71	120 50	160 40	187** 27	206** 19	218** 12	226** 7	233** 7								24
9	66 66	119 53	157 38	183 26	204** 21	217** 13	225** 8	231** 6	236** 5							10
10	66 66	114 48	149 35	177 28	200** 23	215** 15	227** 12	235** 9	243** 7	248 6						8
11	72 72	119 47	152 33	177 25	204 27	220 16	231 11	244 12	250 5	257 7	263 6					3
12	79 79	119 40	141 22	166 24	196 31	206 9	213 7	229 16	243 14	252 9	256 5	261 5				1
13	57 57	101 44	123 21	144 21	159 16	180 21	195 15	200 5	215 15	223 8	228 5	231 3	233 2			1
14	64 64	118 54	164 46	192 28	202 10	214 12	229 15	231 2	236 5	238 2	241 2	243 2	246 3	248 2		1
15	76 76	145 69	162 17	176 14	187 11	198 11	200 2	208 8	217 8	219 3	222 3	227 5	230 3	233 3	235 2	1
Moyenne	68** 68**	118** 50**	159** 41**	186** 27**	203** 17**	215** 12**	224** 9	232** 8	239** 7	246** 6	248 5	240 4	236 2	240 2	235 2	
N	768	678	551	476	405	273	127	49	25	15	7	4	3	2	1	

♀

Groupe d'âge	ANNULUS 1	2	3	4	5	6	7	8	9	10	11	12	13	N
1	74 74													153
2	69 69	121** 52**												255
3	71 71	126** 55**	168** 42**											170
4	72 72	128** 56**	176** 48**	201** 25										321
5	69 69	122 53	170** 48**	203** 33**	222** 19**									264
6	70 70	124** 54**	169** 45**	203** 34**	222** 19**	235** 13**								157
7	69 69	123** 54**	167** 44**	205** 38**	227** 22**	243** 16**	253** 10							60
8	66 66	122 56	169 47	204** 35**	227** 23	240** 13	251** 11	258** 7						14
9	70 70	120 50	165 45	198 33	227** 29	244** 17	255** 11	261** 6	267** 6					5
10	87 87	140 53	188 46	224 38	250** 26	266** 16	279** 12	284** 5	289** 4	293 4				2
13	62 62	115 53	151 36	186 35	211 25	229 18	243 14	251 9	258 7	263 4	269 7	274 4	276 2	1
Moyenne	71** 71**	124** 54**	171** 46**	203** 31**	223** 19**	238** 14**	253** 10	261** 6	271** 6	283** 4	269 7	274 4	276 2	
N	1402	1249	994	824	503	239	82	22	8	3	1	1	1	

FIG. 2. Longueurs (chiffre du haut dans une case) et accroissements (chiffre du bas dans la même case) à chaque annulus, pour les perchaudes des différents groupes d'âge capturées de 1967 à 1970. Deux astérisques signifient que les mâles diffèrent statistiquement des femelles ($P < 0.01$).

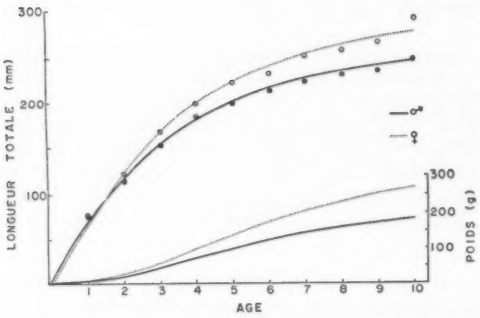

FIG. 3. Croissance en longueur et en poids des perchaudes de la Grande Anse.

TABLEAU 1. Comparaison statistique de la longueur moyenne aux différents annuli pour les femelles adultes et juvéniles des différentes classes d'âge. Entre parenthèses, on donne les effectifs; ** = différences significatives ($P < 0.01$).

Classe d'âge	Annulus	Juvéniles	Adultes
1962	1	71(3)	70(64)
6 ans à	2	123(3)	124(64)
la capture	3	150(3)	170(64)
	4	177(3)	207(64)**
	5	187(3)	223(64)**
	6	198(3)	238(64)**
1963	1	70(35)	72(187)
4 ans à	2	125(35)	129(187)
la capture	3	175(35)	181(187)**
	4	197(35)	205(187)**
1963	1	61(6)	71(85)
5 ans à	2	111(6)	127(85)**
la capture	3	165(6)	174(85)
	4	185(6)	198(85)
	5	206(6)	219(85)
1964	1	75(23)	78(23)
3 ans à	2	133(23)	136(23)
la capture	3	169(23)	175(23)
1964	1	69(13)	78(40)**
4 ans à	2	130(13)	137(40)
la capture	3	162(13)	172(40)
	4	191(13)	203(40)
1965	1	66(33)	68(23)
3 ans à	2	115(33)	120(23)
la capture	3	158(33)	168(23)**
1965	1	64(25)	73(21)**
4 ans à	2	115(25)	128(21)**
la capture	3	160(25)	166(21)
	4	191(25)	198(21)
1966	1	71(62)	75(6)**
3 ans à	2	128(62)	137(6)**
la capture	3	171(62)	188(6)**

oscille légèrement, d'un mois à l'autre, de chaque côté de la moyenne annuelle, 0.45%. Chez les mâles et les femelles adultes, le rapport gonosomatique demeure inférieur à 1% en juin, juillet, et août. Chez les mâles, il augmente brusquement à 6% en septembre, pour diminuer et se maintenir à 5% de novembre jusqu'à la fraye, qui a lieu fin avril, début mai, après le départ des glaces; le testicule demeure laitant durant tout le mois de mai. Chez les femelles adultes, le rapport gonosomatique

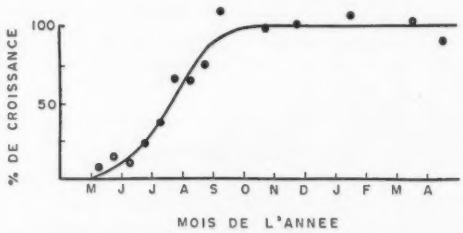

FIG. 4. Croissance saisonnière exprimée en pourcentage de la croissance annuelle pour l'ensemble des classes d'âge et des années de collection.

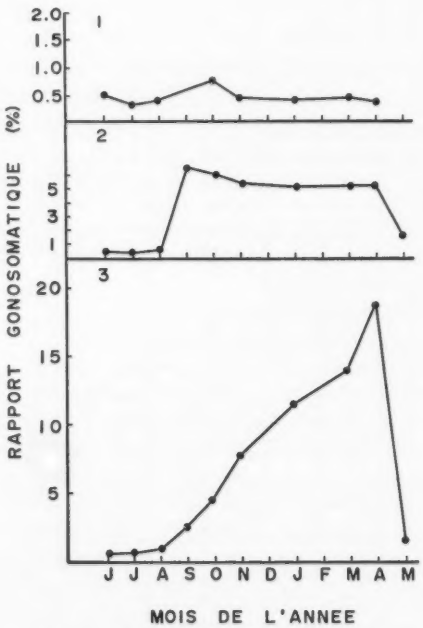

FIG. 5. Rapport gonosomatique aux différents mois de l'année pour les femelles juvéniles (1), les mâles adultes (2) et les femelles adultes (3).

TABLEAU 2. Croissance saisonnière des perchaudes de la Grande Anse; pour les différents groupes d'âge et aux différentes périodes de l'année; on donne la croissance absolue en mm (chiffre du haut) et le pourcentage de croissance (chiffre du bas) réalisés depuis la formation du dernier annulus.

Période de l'année		Groupe d'âge						
		1	2	3	4	5	6	7
1967								
Juin	1–15	9.0	7.1	3.3	1.0	0.1	0.0	0.8
		16.8	17.0	11.5	5.6	1.0	0.0	11.1
Juin	16–30	15.3	12.7	8.3	3.8	2.3	1.4	1.0
		28.4	30.1	29.5	22.1	17.7	16.3	14.4
Juillet	1–15	–	22.1	23.7	8.0	4.0	1.4	1.6
		–	52.4	83.8	46.2	33.1	16.9	22.9
Juillet	16–31	34.5	25.0	24.1	12.0	6.9	5.6	4.4
		64.3	59.3	85.3	69.3	53.7	66.3	64.3
Août	1–15	38.8	31.4	20.9	10.1	9.7	2.4	–
		72.3	74.6	74.0	58.3	75.4	28.3	–
Août	16–31	–	36.3	21.4	14.7	9.5	6.8	4.0
		–	86.2	75.8	85.3	74.1	80.6	58.1
Septembre	1–15	–	–	31.7	22.6	12.5	7.5	12.9
		–	–	112.2	131.3	97.3	89.7	188.9
Octobre	16–31	–	27.8	29.5	18.6	15.7	8.7	–
		–	66.1	104.3	107.9	122.5	103.5	–
Novembre	16–30	62.1	38.4	25.2	17.1	11.5	8.2	4.7
		115.8	91.3	89.1	98.9	89.8	97.9	69.3
1968								
		–	–	–	18.6	12.2	10.1	–
Janvier	1–31	–	–	–	107.5	95.3	120.2	–
Mars	1–31	–	41.8	29.2	16.3	11.7	6.0	–
		–	99.3	103.2	94.2	92.3	71.4	–
Avril	1–30	58.5	40.4	25.3	15.9	12.2	6.5	5.0
		108.9	96.0	89.4	91.9	95.3	77.4	73.5
Mai	1–15	–	2.5	2.6	1.8	–	0.0	–
		–	6.2	8.4	8.3	–	0.0	
Mai	16–31	4.3	4.9	–	2.1	1.4	0.8	2.5
		7.1	11.9	–	10.0	9.7	8.2	38.6
Juillet	1–15	13.9	21.2	9.4	9.3	3.7	1.7	1.9
		31.1	51.3	30.8	43.2	26.7	17.5	28.6
Août	1–15	–	–	–	15.0	10.4	5.4	3.8
		–	–	–	70.0	75.0	56.0	59.1
Août	16–31	44.8	31.1	21.3	13.1	10.4	6.9	5.3
		82.8	75.2	70.0	61.3	75.0	71.7	80.8
Septembre	16–30	48.5	34.5	29.6	18.4	15.3	10.9	5.8
		89.6	83.4	97.4	86.0	109.9	112.7	90.0
Octobre	16–31	52.5	34.8	23.3	20.4	13.1	11.3	6.0
		97.0	84.1	76.7	95.3	94.1	116.1	92.0
Novembre	16–30	48.6	35.8	35.8	19.4	14.9	9.5	10.1
		89.8	86.6	17.7	90.5	106.7	97.7	155.7
1969								
Janvier	1–30	–	42.9	29.3	17.1	14.8	10.2	6.1
		–	103.6	96.4	79.9	106.5	105.2	93.8
Mars	1–31	–	49.9	32.1	24.9	13.7	9.3	8.6
			120.5	105.6	116.4	98.6	95.9	132.3
Avril	1–30	–	41.2	30.9	19.4	12.4	8.5	4.5
		–	99.5	101.6	90.5	89.2	87.7	69.2
Mai	1–15	–	0.1	0.0	0.0	0.0	0.0	0.0
Juin	16–30	6.3	7.1	5.0	2.3	2.8	1.6	0.0
Juillet	1–15	18.6	9.3	6.9	8.1	4.5	5.1	4.3
Octobre	1–15	52.3	35.6	24.4	16.3	12.7	9.2	7.8

TABLEAU 3. Poids moyen, indice de condition moyen ($\overline{K}$), et effectif (N) aux différentes classes de longeur.

LT (*mm*)	Mâles			Femelles			Sexes groupes		
	Pds (*g*)	$\overline{K}$	N	Pds (*g*)	$\overline{K}$	N	Pds (*g*)	$\overline{K}$	N
50–59	1.9	1.131	11	1.9	1.067	15	1.9	1.094	26
60–69	3.2	1.126	20	3.1	1.114	32	3.2	1.118	52
70–79	4.4	1.047	83	4.5	1.061	91	4.5	1.054	174
80–89	6.5	1.113	89	6.6	1.100	116	6.6	1.105	205
90–99	9.7	1.160	55	9.4	1.153	77	9.5	1.156	132
100–109	13.4	1.202	37	13.6	1.220	49	13.5	1.212	86
110–119	16.7	1.139	23	19.0	1.239	44	18.2	1.205	67
120–129	24.3	1.219	23	25.1	1.254	39	24.8	1.241	62
130–139	29.7	1.217	114	29.8	1.211	152	29.8	1.214	266
140–149	36.0	1.204	126	36.6	1.208	165	36.3	1.206	291
150–159	44.4	1.214	86	44.4	1.213	128	44.4	1.213	214
160–169	54.5	1.233	58	55.9	1.246	126	55.5	1.242	184
170–179	65.4	1.226	46	64.2	1.208	120	64.5	1.213	166
180–189	77.9	1.243	39	76.2	1.221	72	76.8	1.229	111
190–199	100.1	1.341	57	98.0	1.320	97	98.8	1.328	154
200–209	114.4	1.325	174	114.6	1.330	183	114.5	1.328	357
210–219	127.2	1.287	182	129.3	1.305	269	128.4	1.298	451
220–229	141.8	1.264	160	145.3	1.292	259	143.9	1.281	419
230–239	161.9	1.262	92	166.3	1.295	184	164.8	1.284	276
240–249	181.4	1.259	44	188.5	1.286	135	186.7	1.280	179
250–259	205.2	1.249	14	214.6	1.312	58	212.8	1.300	72
260–269	260.6	1.449	2	238.1	1.299	54	238.9	1.304	56
270–279	209.8	1.028	3	266.8	1.304	25	260.7	1.276	28
280–289				292.7	1.300	7	292.7	1.300	7
310–319				412.0	1.293	1	412.0	1.293	1

augmente régulièrement de 4 à 19% de septembre à avril.

A cause de la sélectivité des engins de pêche (spécialement du filet maillant de 2½ po.), nous avons restreint notre étude de la condition aux femelles adultes (Fig. 6). Chez ces poissons, l'indice de condition ordinaire K atteint son maximum en hiver, diminue après la fraye et aussi pendant l'été et augmente en automne. En groupant les résultats pour 1967, 1968, et 1969 et en exprimant chaque valeur de K en pourcentage de la plus forte valeur, observée en mars, on peut illustrer simultanément les variations de la condition et du rapport gonosomatique (Fig. 7). Les très fortes valeurs hivernales de K sont associées à des rapports gonosomatiques élevés; par contre, si nous ne tenons pas compte des gonades, la condition est à son maximum en juin.

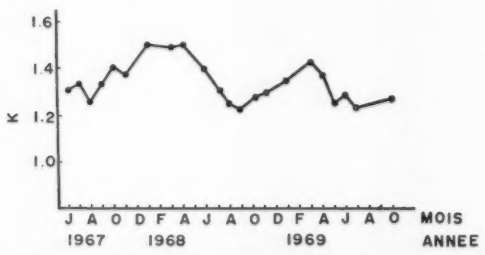

FIG. 6. Variations mensuelles de l'indice de condition K pour les femelles adultes.

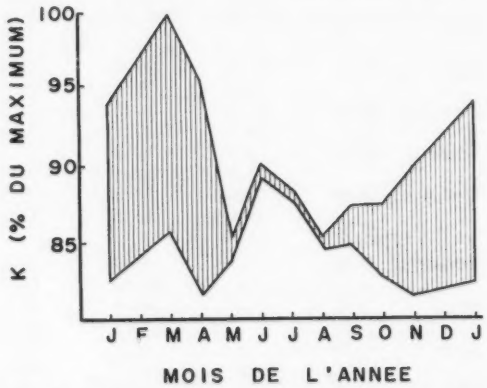

FIG. 7. Cycle annuel de K suivant que l'on inclut les gonades (ligne supérieure), ou que l'on exclut les gonades; la bande hachurée représente le rapport gonosomatique.

La moyenne générale de K, calculée à partir de la longueur standard moyenne des perchaudes de la Grande Anse et du poids correspondant, est 1.976.

Discussion

Certains des résultats obtenus ici confirment quelques aspects bien connus de la biologie de la perchaude; par exemple, les femelles grandissent plus rapidement que les mâles et atteignent une longueur plus grande; les individus à croissance rapide deviennent adultes à un plus jeune âge que les individus à croissance lente; la pente de l'équation longueur–poids logarithmique est supérieure à 3; l'ordre de grandeur des rapports gonosamotiques observés ici coïncide avec celui des données publiées à ce sujet.

Par ailleurs, il est intéressant de mentionner que les perchaudes de la Grande Anse maintiennent un taux de croissance excellent si on les compare aux perchaudes de différents autres lacs et rivières du Québec (Grimaldi MS 1967). De plus, en comparant nos données à celles de Préfontaine (MS 1941), nous avons constaté qu'en 30 ans, l'allure de la courbe de croissance des perchaudes de la Grande Anse a changé: en 1941, les perchaudes avaient un rythme de croissance plus lent durant les premières années et elles atteignaient des tailles plus grandes à 8, 9 et 10 ans. Il ne semble pas cependant que la durée de la période de croissance saisonnière ait changé; en effet, Fry et al. (MS 1941) ont montré que la croissance estivale des jeunes perchaudes de l'année était pratiquement terminée en septembre et ceci coïncide avec nos observations. Enfin, mentionnons que les perchaudes femelles de la Grande Anse atteignent leur plus haut degré d'embonpoint en hiver et que les fluctuations saisonnières de K sont surtout associées aux fluctuations du poids des gonades; ces résultats diffèrent ainsi de ceux de LeCren (1951); les perches (*Perca fluviatilis*) du lac Windermere atteignaient leur plus haut degré d'embonpoint à la fin de l'été.

Remerciements

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Effects of Dressing and Cooking on DDT Concentrations in Certain Fish from Lake Michigan[1]

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REINERT, R. E., D. STEWART, AND H. L. SEAGRAN. 1972. Effects of dressing and cooking on DDT concentrations in certain fish from Lake Michigan. J. Fish. Res. Bd. Canada 29: 525–529.

Concentrations of DDT residues were highest in parts of the body with the highest oil content in four species of fish from Lake Michigan: yellow perch (*Perca flavescens*), bloater (*Coregonus hoyi*), lake trout (*Salvelinus namaycush*), and coho salmon (*Oncorhynchus kisutch*). Dressing reduced the DDT residues and oil content by more than 90% in yellow perch but had little effect in the other three species. The concentration of DDT residues in bloaters was changed little by smoking but was reduced 64–72% by other methods of cooking: from 8.0 ppm (raw) to 2.2 ppm after frying in corn oil; from 10.7 to 3.9 ppm after frying in lard; and from 9.1 to 3.2 ppm after broiling. The concentration of DDT residues in fillets of yellow perch changed only from 0.3 ppm (raw) to 0.4 or 0.5 ppm after baking, frying, or broiling.

REINERT, R. E., D. STEWART, AND H. L. SEAGRAN. 1972. Effects of dressing and cooking on DDT concentrations in certain fish from Lake Michigan. J. Fish. Res. Bd. Canada 29: 525–529.

Les teneurs en résidus de DDT sont plus élevées dans les parties du corps les plus riches en huile chez quatre espèces de poissons du lac Michigan: la perchaude (*Perca flavescens*), le cisco de fumage (*Coregonus hoyi*), le touladi (*Salvelinus namaycush*) et le saumon coho (*Oncorhynchus kisutch*). Le parage réduit de plus de 90% les résidus de DDT et la teneur en huile de la perchaude, mais n'a que peu d'effet sur les trois autres espèces. La teneur en résidus de DDT des ciscos n'est que peu affectée par le fumage, mais est réduite de 64 à 72% par les autres méthodes de cuisson: de 8.0 ppm (à l'état cru) à 2.2 ppm après friture dans l'huile de maïs; de 10.7 à 3.9 ppm après friture au saindoux; et de 9.1 à 3.2 ppm après cuisson sur le gril. La teneur en résidus de DDT des filets de perchaude n'a changé que de 0.3 ppm (à l'état cru) à 0.4 ou 0.5 ppm après cuisson au four, en friture ou sur le gril.

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FISH from many localities in the United States, including Lake Michigan, contain DDT residues in excess of the 5-ppm interim administrative limit for fish set hy the U.S. Food and Drug Administration (Henderson et al. 1969; Poff and Degurse 1970). Little information is available, however, on the distribution of DDT residues in the fish or on the effects of different methods of processing and cooking on DDT concentrations.

The present study concerns the effects of dressing on DD Tcontent, as determined by measuring the concentration of DDT residues in different body parts of yellow perch (*Perca flavescens*), bloaters (*Coregonus hoyi*), lake trout (*Salvelinus namaycush*), and coho salmon (*Oncorhynchus kisutch*); the effects of brining and smoking on concentrations of DDT residues in bloaters; and the effects of frying, baking, or broiling on the concentrations in bloaters and yellow perch.

Procedures

Fish collected in Lake Michigan by the U.S. Fish and Wildlife Service and the Michigan Department of Natural Resources were frozen immediately after capture and stored at –36.7 C. Concentrations of DDT residues were determined for raw fish (whole, eviscerated, filleted, or steaked) and for cooked fish after smoking, frying, baking, or broiling.

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Two methods of analysis were used in measuring DDT concentrations. In yellow perch and bloaters residues of DDT (*p,p'* DDE and *p,p'* DDT) were determined by saponifying samples in alcoholic KOH and then extracting with hexane. Since saponification converts *p,p'* DDT into *p,p'* DDE, the results for these species are expressed only as the total of the two isomers. In lake trout and coho salmon, residues of DDT (*p,p'* DDE, *p,p'* DDD, *o,p'* DDT, and *p,p'* DDT) were extracted by homogenizing samples in a 1:1 mixture of isopropenol and benzene and then extracting with hexane. The extraction methods and analytical procedures were described by Reinert (1970). Insecticide concentrations are expressed as parts per million (micrograms of insecticide per gram wet weight of fish).

Percentages of oil and water (wet weight) were determined for all samples analyzed for DDT residues. To determine percentage oil, 10-g samples of fish were homogenized in a 1:1 mixture of isopropenol and benzene for 5 min; 30 ml of hexane were added and the samples were boiled slowly on a water bath for 45 min; after cooling, the solvent extract was poured off and concentrated to 30 ml; 15 ml were transferred to a tared aluminum dish and the solvent was evaporated in a hood at room temperature; and the aluminum dish was then weighed and the percentage oil calculated. To determine percentage water, a 5-g wet weight sample of fish was placed on a tarred aluminum weighing dish, heated at 110 C for 18 hr, cooled in a desiccator, weighed, and the percentage water calculated.

To determine the effects of dressing on concentrations of DDT residues, oil, and water in bloaters and yellow perch, the fish were analyzed after evisceration (bloaters) and after filleting (bloaters and perch). Values for whole fish were obtained by combining the amounts in the viscera (or viscera and other offal) with the amounts in the eviscerated fish or in the fillets.

To determine the effects of dressing on lake trout and coho salmon, 24-mm thick steaks were cut just anterior to the dorsal fin from frozen whole fish, and either the whole steak or portions of the steak and the remainder of the fish were analyzed for DDT residues and oil.

To determine the effects of smoking, bloaters were analyzed for DDT residues, oil, and water after each stage of preparation (evisceration, brining, and smoking). After evisceration, the fish were brined (two parts of 34% [34° salimeter] brine per part of fish, by weight) for 15 hr at −1.1 C. During smoking, the internal temperature of the fish was raised to 82.2 C and held for ½ hr. A glass jar was hung beneath each fish to collect drippings for analysis of DDT and oil.

In the cooking experiments, fillets of bloaters and yellow perch and the processing waste from each fish were analyzed for DDT residues, oil, and water; the fillet from the right side was analyzed raw and that from the left side after cooking. Chub fillets were pan fried in 120 ml of corn oil or lard for 2½ min on each side, or broiled for 6 min on each side. Perch fillets were baked at 176.7 C for 10 min, broiled on each side for 3–4 min, or pan fried in 120 ml of corn oil for 3–4 min on each side.

Results

Effects of Dressing

Filleting of yellow perch removed more than 90% of the DDT residues and oil; evisceration and filleting of bloaters, however, had little effect on concentration of DDT residues or oil content (Table 1).

As in the bloaters, the evisceration of lake trout had little effect on concentration of DDT residues or percentage oil content. As an average for 62 fish, the concentration of DDT residues (ppm) was 16.4

Table 1. Average and (in parentheses) ranges for weight and DDT (*p,p'* DDT and *p,p'* DDE) and oil content in whole, eviscerated, and filleted bloaters and in whole and filleted yellow perch.

Species and form	Weight (*g*)	DDT (*ppm*)	Oil (%)
Yellow perch, 24 fish			
Whole	200.0 (139–270)	3.9 (2.0–6.2)	6.6 (4.1–7.7)
Fillet	37.9 (28.5–46.0)	0.3 (0.1–0.6)	0.6 (0.2–1.0)
Bloater (medium), 7 fish			
Whole	180.6 (150–230)	9.9 (5.6–13.1)	18.8 (14.8–21.3)
Eviscerated	156.4 (125–203)	10.0 (5.1–13.5)	18.3 (14.1–21.4)
Bloater (large), 18 fish			
Whole	258.4 (200–380)	8.1 (4.4–16.0)	28.1 (24.5–32.7)
Fillet	69.6 (49.1–103.1)	9.3 (5.2–18.2)	27.9 (18.9–36.5)

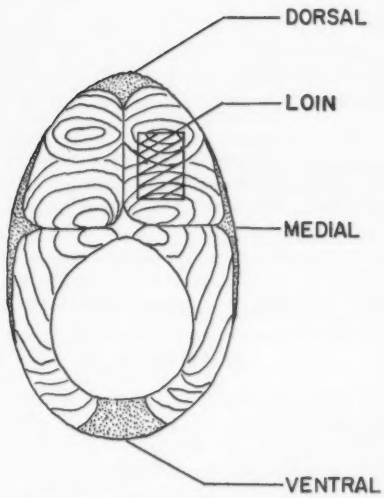

FIG. 1. Portions of coho salmon and lake trout steaks examined for DDT and oil.

± 1.5 (95% confidence interval) in whole fish and 17.0 ± 1.6 in steaks; percentage oil was 20.8 ± 1.4 in the whole fish and 22.0 ± 1.6 in the steaks.

The analysis of various parts of steaks cut from 10 coho salmon and 3 lake trout showed that the concentrations of DDT residues in the dorsal, medial, and ventral areas (Fig. 1) were about 7–12 times higher than in the loin in coho salmon, and 4–8.5 times higher than in the loin in lake trout (Table 2).

EFFECTS OF BRINING AND SMOKING

Neither brining nor smoking of bloaters had a noticeable effect on the concentrations of DDT residues or on oil content of the fish (Table 3). Although smoked bloaters contained 36% less DDT (by weight) than the brined fish, the percentage of weight lost during smoking was closely similar (35%); consequently the concentration of DDT in the smoked product (9.0 ppm) differed little from that in the eviscerated (10.0 ppm) or brined (9.2 ppm) fish. Oil drippings collected during smoking contained an average of 58.4 ppm DDT residues.

TABLE 2. Average and (in parentheses) range of DDT (*p,p'* DDT, *p,p'* DDD, *o,p'* DDT, and *p,p'* DDE) and oil content in different parts of raw 24-mm thick steaks from 10 coho salmon and 3 lake trout (Portions of the steaks examined are shown in Fig. 1).

Portions of steaks analyzed	Coho salmon		Lake trout	
	DDT (*ppm*)	Oil (%)	DDT (*ppm*)	Oil (%)
Whole steak	14.9 (10.2–19.2)	13.2 (13.8–20.4)	17.4 (13.3–20.9)	25.7 (20.8–30.4)
Dorsal	61.1 (37.8–83.1)	62.1 (58.3–65.2)	67.3 (61.3–71.8)	66.7 (44–86)
Loin	5.6 (3.2–8.4)	5.4 (2.9–6.6)	7.9 (5.4–10.6)	9.1 (7.8–11.2)
Medial	41.1 (32.7–46.3)	44.5 (36.2–65.6)	32.0 (17.2–41.8)	37.7 (34.0–42.0)
Ventral	66.0 (52.2–84.2)	67.0 (59.2–74.3)	55.0 (34.0–72.2)	63.0 (54.0–74.0)

TABLE 3. Average and (in parentheses) ranges for weights and DDT (*p,p'* DDT and *p,p'* DDE), oil, and water contents in whole, eviscerated, brined, and smoked bloaters (Each average and range shown is for a sample of seven fish).

Form of fish	Weight (*g*)	DDT (*ppm*)	Oil (%)	Water (%)
Whole	180.6 (150–230)	9.9 (5.6–13.1)	18.8 (14.8–21.3)	65.5 (63.5–68.9)
Eviscerated	156.4 (125–203)	10.0 (5.1–13.5)	18.3 (14.1–21.4)	65.4 (62.9–68.9)
Brined	160.7 (126–234)	9.2 (7.3–13.5)	15.4 (12.2–20.4)	67.2 (64.6–71.5)
Smoked	103.9 (72–151)	9.0 (6.7–14.8)	17.7 (13.1–23.2)	57.3 (51.2–61.6)

EFFECTS OF OTHER COOKING METHODS

The amount of DDT residues lost by bloater fillets during cooking was large and the loss of weight relatively small; consequently, the concentration of residues decreased substantially (64–72%) in the cooked fillets: from 8.0 ppm (raw) to 2.2 ppm after frying in corn oil; from 10.7t o 3.9 ppm after frying in lard; and from 9.1 to 3.3 ppm after broiling (Table 4). Losses of oil during cooking by the

TABLE 4. Average and (in parentheses) ranges for weight and DDT (*p,p'* DDT and *p,p'* DDE), oil, and water contents of raw and cooked fillets and offal (whole fish minus the fillet) of bloaters and yellow perch (In each cooking test, eight bloaters or six yellow perch were used).

Cooking method and form	Weight (*g*)	DDT (*ppm*)	Oil (%)	Water (%)
		Bloater		
Fried in corn oil				
Raw fillet	77.2 (62.8–103.1)	8.0 (5.2–11.4)	27.9 (24.1–31.4)	57.5 (54.1–61.5)
Cooked fillet	54.8 (40.6–81.1)	2.2 (1.3–3.8)	12.5 (8.9–20.8)	66.8 (57.2–70.0)
Offal (raw)	125.8 (97.7–173.5)	5.2 (3.1–8.1)	29.6 (22.9–41.6)	57.3 (47.5–62.6)
Fried in lard				
Raw fillet	60.7 (49.1–73.6)	10.7 (7.3–18.2)	30.7 (22.8–36.5)	59.2 (50.9–62.1)
Cooked fillet	41.6 (32.7–54.1)	3.9 (2.5–5.7)	12.4 (6.7–16.8)	65.1 (57.8–73.1)
Offal (raw)	101.4 (80.2–131.9)	7.7 (5.7–9.3)	24.4 (20.8–29.0)	61.3 (56.9–64.3)
Broiled				
Raw fillet	70.6 (55.4–86.5)	9.1 (5.4–14.0)	26.7 (18.6–31.4)	59.3 (54.9–66.6)
Cooked fillet	51.2 (41.1–60.2)	3.3 (2.6–4.3)	12.3 (8.6–16.6)	67.8 (63.5–72.2)
Offal (raw)	114.3 (102.3–129.4)	7.0 (5.7–9.3)	27.8 (24.8–31.1)	59.1 (56.7–61.4)
		Yellow perch		
Fried in corn oil				
Raw fillet	36.8 (32.5–44.5)	0.3 (0.1–0.5)	0.6 (1.0–0.2)	78.6 (76.7–79.1)
Cooked fillet	26.6 (18.5–39.0)	0.4 (0.1–0.6)	3.9 (2.7–5.9)	71.2 (64.8–74.8)
Offal (raw)	124.3 (87.0–181.0)	6.4 (3.3–9.0)	10.7 (8.4–12.6)	70.2 (66.8–73.4)
Broiled				
Raw fillet	39.0 (34.0–43.0)	0.3 (0.1–0.6)	0.8 (0.4–1.0)	79.1 (77.6–80.3)
Cooked fillet	22.4 (18.0–25.0)	0.5 (0.2–1.0)	0.9 (0.5–1.6)	68.5 (66.0–71.5)
Offal (raw)	124.4 (94.0–153.5)	5.6 (2.8–9.7)	10.5 (8.3–12.2)	70.4 (68.1–74.8)
Baked				
Raw fillet	37.8 (28.5–46.0)	0.3 (0.1–0.6)	0.5 (0.4–0.9)	79.9 (78.3–81.1)
Cooked fillet	26.6 (22.0–32.5)	0.4 (0.2–0.9)	0.8 (0.5–1.0)	75.3 (71.4–77.4)
Offal (raw)	123.2 (82.0–157.5)	7.0 (4.1–10.8)	10.1 (6.2–12.9)	70.3 (66.8–71.5)

different methods ranged from 54 to 60%. The concentration of DDT residues in the cooking lard increased from 0.2 ppm before cooking to 12.8 ppm after cooking, and the concentration in the corn oil increased from nil (nondetectable) before cooking to 10.9 ppm after cooking.

In perch fillets, the concentration of DDT residues changed little after pan frying, broiling, and baking — only from 0.3 to 0.4 ppm in the baked and fried fillets and from 0.3 to 0.5 ppm in the broiled fillets (Table 4). Oil content of fillets was not changed appreciably by baking and broiling; however, the oil in fillets fried in corn oil increased from 0.6% before cooking to 3.9% after cooking.

Conclusions

Parts of the fish that contained the highest concentrations of DDT residues contained the highest concentrations of oil. Since the location of oil in fish varies among species, a method of cleaning that lowers the DDT residues in one species may not lower it in others. Filleting removed most of the DDT residues in yellow perch because most of the oil is in the offal; the residues were not effectively lowered, however, by the dressing of bloaters, coho salmon, and lake trout, in which oil is more evenyl distributed in the body. Analysis of DDT residues in different parts of raw steaks of coho salmon and lake trout indicated that trimming of the fatty areas along the back, lateral line, and the belly would substantially lower the DDT residues.

The methods of cooking and smoking evaluated here generally caused a loss of DDT residues directly proportional to the amounts of oil lost. Changes in the concentration of DDT residues after cooking depend on the relation between the amount of DDT residues lost and the amount of weight lost; only when the percentage of DDT residues lost is greater than the percentage weight lost is there a drop in the concentration of DDT residues.

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Morphology and Enzyme Histochemistry in the Liver of Largemouth Bass (*Micropterus salmoides*)

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HINTON, D. E., R. L. SNIPES, AND M. W. KENDALL. 1972. Morphology and enzyme histochemistry in the liver of largemouth bass (*Micropterus salmoides*). J. Fish. Res. Bd. Canada 29: 531–534.

Livers of 27 bass collected from streams and an impoundment in Kentucky were subjected to light and electron microscopic as well as enzyme histochemical examination. The connective tissue framework of the liver was primarily collagen and reticulum. Elastic lamellae were seen in hepatic arteries. Hepatic parenchyma was arranged in dual-plated muralia. Hepatocytes contained glycogen, endoplasmic reticulum, mitochondria, and a homogeneous nucleus with one prominent nucleolus. Pancreatic acini were observed in walls and perivascular connective tissue of portal veins. No distinct lobular pattern of parenchyma was observed. The enzyme glucose-6-phosphatase was abundant in cytoplasm of hepatocytes usually forming a perinuclear cuff. Alkaline phosphatase was determined in the sinusoidal border of hepatocytes and in walls of central veins. Differentiation of portal veins from central veins was made on the basis of proximity to the hepatic artery and bile duct.

HINTON, D. E., R. L. SNIPES, AND M. W. KENDALL. 1972. Morphology and enzyme histochemistry in the liver of largemouth bass (*Micropterus salmoides*). J. Fish. Res. Bd. Canada 29: 531–534.

Nous avons examiné en microscopie optique et électronique et soumis à l'analyse histochimique des enzymes le foie de 27 achigans à grande bouche provenant de cours d'eau et d'un réservoir de retenue du Kentucky. La charpente de tissu connectif du foie est constituée surtout de collagène et de reticulum. On voit des lamelles élastiques dans les artères hépatiques. Le parenchyme hépatique est agencé en muralia à deux lames. Les cellules hépatiques contiennent du glycogène, un reticulum endoplasmique, des mitochondries et un noyau homogène possédant un nucléole proéminent. Nous avons remarqué des acini pancréatiques dans la paroi et le tissu connectif périvasculaire des veines portes. Le parenchyme semble dépourvu de lobulation distincte. L'enzyme glucose-6-phosphatase est abondante dans le cytoplasme des cellules hépatiques qui forment généralement un parement autour du noyau. Nous avons dosé la phosphatase alcaline des points de rencontre des sinusoïdes et des cellules hépatiques ainsi que celle des parois des veines centrales. Nous nous sommes basés, pour différencier les veines portes des veines centrales, sur leur proximité de l'artère hépatique ou du conduit biliaire.

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DESPITE increased interest in the effects of pesticide and heavy metal toxins on fishes, there have been relatively few studies concerned with the morphology of the liver, an organ of detoxification (Hogan and Knowles 1968). The occurrence of trout hepatoma in a wide variety of locations prompted study of livers from normal and affected species. No such disaster has occurred with the largemouth bass (*Micropterus salmoides*); however, the extensive application of this species in sport fisheries and the question of alteration by aquatic toxins have led us to attempt description of the hepatic morphology and enzyme histochemistry.

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Materials and Methods

FISH

In April and May 1970–71 a total of 27 bass 170–624 g and 14.9–30.5 cm long were collected by electroshocking and seining from tributaries of the Salt River, Spencer County, Kentucky, and Green River Reservoir, Adair County, Kentucky. Rapid stream-side dissection was performed and livers were placed in appropriate solutions (see below) for subsequent examination.

HISTOLOGIC TECHNIQUES

Light microscopy — Tissues for lipid analysis were fixed in 10% formalin, frozen and sectioned on a cryostat at 12 μ. Both Oil Red O and Sudan Black dyes were

used to demonstrate fat. Tissues for routine histologic examination were fixed for 24 hr in Bouin's fixative, transferred to 70% alcohol for storage and subsequently dehydrated in alcohol, cleared in xylene, and embedded in paraffin. Sections were cut at 6 μ on a rotary microtome. The PAS (periodic acid-Schiff's reagent), Mallory aniline blue (for collagenous fibers), and a silver method (for reticular fibers) were used to show connective tissue. Of these only the silver method demonstrated reticular fibers selectively. The fibers designated as reticular were threadlike and displayed an intense argyrophilia (Fig. 4). In the same silver-stained sections the broad collagenous fibers were blue-gray and became muddy red when counterstained with eosin. The argyrophilia (i.e., black) of reticular fibers was not altered by any counterstain. In addition the PAS (with and without diastase-hydrolysis) was used to demonstrate glycogen. These sections were counterstained with hematoxylin for nuclear differentiation and general survey of cytologic architecture. In general these techniques follow those presented by Lillie (1954). The large sizes of the sections and the use of several staining methods provided sufficient material for an extensive study of this organ.

Electron microscopy — For electron microscopic study 1 mm^3 pieces of liver were fixed in 3% glutaraldehyde in phosphate buffer (*p*H 7.4) at 4 C, postfixed in 1% osmium tetroxide, dehydrated in alcohols, and embedded in epoxy resin. Thin sections were cut on a Sorvall MT_2 ultramicrotome. Sections were subsequently stained with uranyl acetate and lead hydroxide and viewed on a Philips 200 electron microscope. To correlate electron and light microscopic observations, thick sections (1 μ) of epoxy embedded material were stained with Schiff's reagent for glycogen.

Histochemical Techniques

Tissues were quick frozen in liquid nitrogen, transported to the laboratory in dry ice, and sectioned on a cryostat at 10 μ. Sections were subsequently stained for alkaline and glucose-6-phosphatase using standard methods (Pearse 1968).

Observations

The hepatic parenchyma existed as a muralium two cells in thickness (Fig. 1). Sinusoids intervened between adjacent cords of hepatocytes (Fig. 2 and 3). Hepatocytes contained abundant glycogen which appeared red with the periodic acid-Schiff's reagent technique. Staining with hematoxylin and eosin was unsuccessful in demonstrating glycogen; thus, the individual hepatocytes appeared extremely vacuolated (Fig. 1).

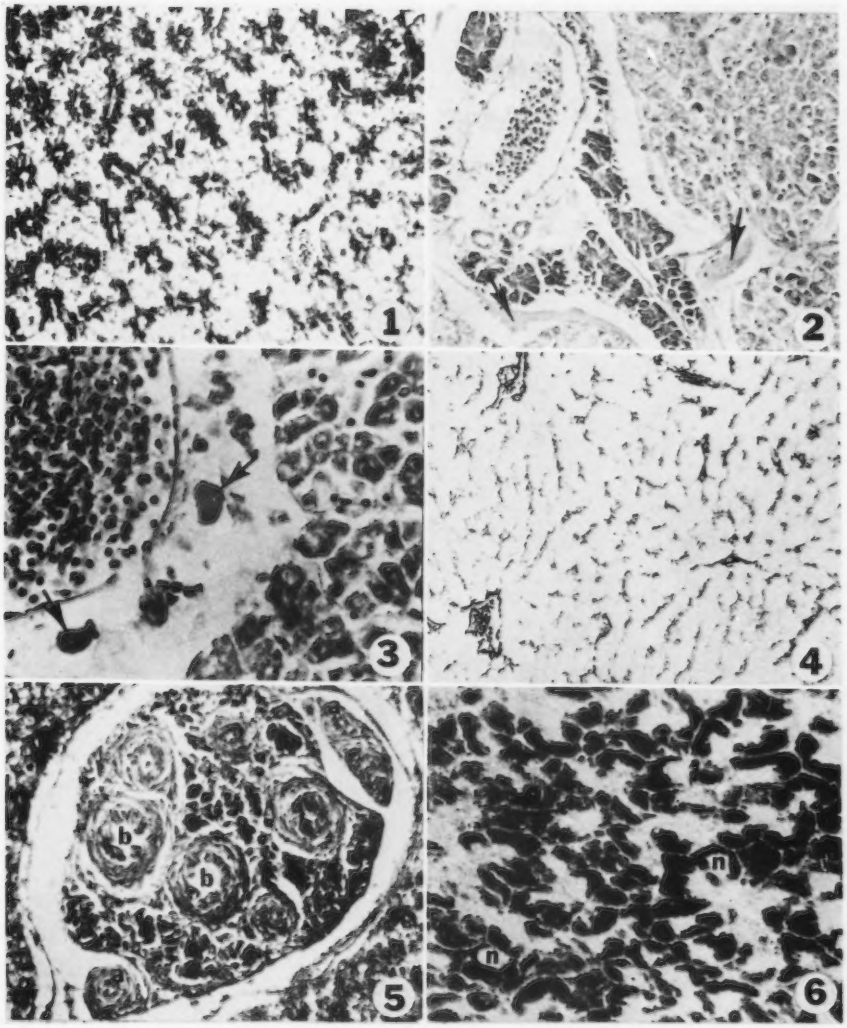
In general the PAS technique with hematoxylin to stain the nuclei was the method of choice for routine survey. The hepatocytes differed in appearance between different fish. Cells in some sections of PAS and hematoxylin stained tissue were vacuolated while others (Fig. 2 and 3) revealed more cytoplasmic basophilia with fewer vacuoles. Cytoplasmic basophilia and glycogen were inversely proportional. When Oil Red O and Sudan Black stains were applied to frozen sections, occasional minute droplets of intracytoplasmic fat were seen. The PAS stained, epon embedded, thick sections revealed the most glycogen (Fig. 6). Thus the contents of the hepatocytes consisted almost entirely of glycogen with a varying amount of cytoplasmic basophilia.

Nuclei (one per cell) appeared homogeneous with a prominent centrally located nucleolus. Abundant red blood cells and an amorphous acidophilic material which was slightly PAS positive were often seen in larger veins or in perivenous spaces between adventitia and surrounding parenchyma (Fig. 2 and 3). Sinusoids were well delineated by the presence of red blood cells. Walls and perivascular connective tissue of portal veins were frequently the site of pancreatic acini (Fig. 2 and 5). The apical portions of the pancreatic acinar cells revealed numerous PAS positive secretory granules. In addition to the pancreatic tissue of portal veins, some bundles were seen (Fig. 5) in which a thick connective tissue border enclosed bile ducts, hepatic arteries, and pancreatic tissue.

The lobular pattern of hepatic parenchymal arrangement commonly seen in mammalian liver was not a finding in this study. Central veins (the initial tributaries of the hepatic veins) were differentiated from portal veins that were frequently associated with bile ducts, hepatic arteries, and pancreatic tissue (Fig. 2).

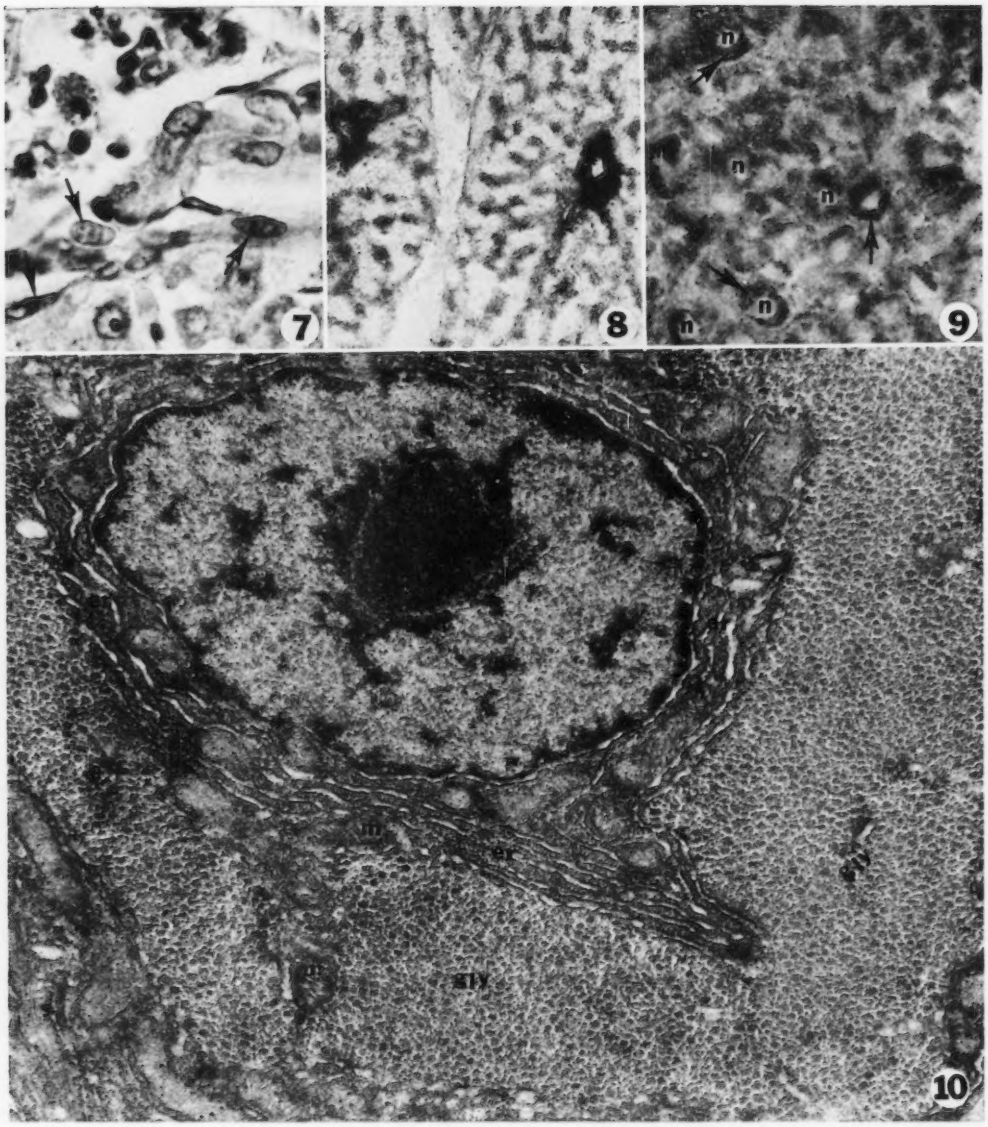
The connective tissue stroma was comprised chiefly of collagen and reticulum with elastic lamellae seen in some hepatic arterioles. The analine blue collagen stain revealed fibers as deep blue bands found in the hepatic capsule and in walls of vessels and bile ducts. Reticular fibers, demonstrable with the silver method were seen in the hepatic capsule, walls of vessels and bile ducts, and in the walls of sinusoids (Fig. 4). These thin reticular fibers appeared to form a mesh pattern around hepatocytes. Pancreatic cells were separated from hepatocytes by a thin septum of connective tissue (Fig. 2). Although the majority of connective tissue within the parenchyma was of the reticular type, some broader fibers staining gray in color with the silver technique were thought to be collagen fibers. Abundant fibroblasts were seen in the perivascular spaces of medium and large diameter veins (Fig. 7).

The typical features of the hepatocytes revealed by electron microscopic examination are shown in Fig. 10. The nuclei revealed a fairly homogeneous nucleoplasm with one prominent centrally located nucleolus. Higher magnification of the nucleoli



FIGURES 1–6.

FIG. 1. Extensive vacuolation of hepatocytes. Cells arranged as cords 2 cells in thickness. Hematoxylin and Eosin ×325; FIG. 2. Hepatocytes less vacuolated. Amorphous material (arrows) is in perivascular space and in vein adjacent to nucleated red blood cells. Basophilic cells in wall of portal vein are pancreatic acinar cells. Periodic acid Schiff's Reagent and Hematoxylin ×325; FIG. 3. Pronounced perivascular space (possibly a fixation artefact) contains nucleated red blood cells and amorphous deposits (arrows). Hepatocytes only slightly vacuolated. Periodic acid Schiff's Reagent and Hematoxylin ×400; FIG. 4. Reticular network of connective tissue in liver. Fibers delineate sinusoids and are found also in walls of hepatic vessels. Silver impregnation ×325; FIG. 5. Well circumscribed bundle containing bile ducts (b), hepatic arteries(a), and basophilic cells of hepatopancreas. Periodic acid Schiff's Reagent and Hematoxylin ×325; FIG. 6. Nuclei (n) are surrounded by dense glycogen deposits. 1-μ thick section stained with Schiff's Reagent ×950.



FIGURES 7–10.

FIG. 7. Fibroblasts (arrows) at junction of medium size size vein and sinusoid. Periodic acid Schiff's Reagent and Hematoxylin ×893; FIG. 8. Alkaline phosphatase in central vein and sinusoids. ×376; FIG. 9. Glucose-6-phosphatase in hepatocytes. Dye forms perinuclear cuff about nuclei (n). ×893; FIG. 10. Electron micrograph of typical hepatocyte. Nucleus has homogeneous nucleoplasm with one prominent nucleolus. Nucleus is surrounded by cuff of endoplasmic reticulum (ER) and mitochondria (M). Remainder of cytoplasm is site of glycogen deposits (gly); imperfectly divided by strands of endoplasmic reticulum and mitochondria. ×21,150.

showed these structures to consist of the more electron lucent pars amorpha and a fibrillar nucleolonema. Adjacent to each nucleus was a cuff of dense cytoplasm containing endoplasmic reticulum and mitochondria. Extensions of this dense cytoplasmic material were found separating sites of glycogen deposition. The chief components of the cuff and the extensions were granular endoplasmic reticulum and tubular mitochondria.

Large deposits of glycogen (Fig. 10) in the typical rosette pattern were common features of hepatocytes. Thick sections (1 μ) (Fig. 6) revealed this component far better than the similarly stained paraffin embedded tissue (Fig. 2 and 3). Frequently, glycogen deposition was so extensive that it became the most prominent cytologic feature. Bile canaliculi were found between adjacent hepatocytes.

Central veins revealed abundant alkaline phosphatase. The sinusoidal edges of hepatocytes also revealed some activity (Fig. 8). Glucose-6-phosphatase was found throughout the hepatic parenchyma and generally formed a cuff about the nuclei (Fig. 9). This perinuclear cuff resembled the pattern seen in the cuff of endoplasmic reticulum and mitochondria (Fig. 10).

Discussion

The dual plated muralium of branching and anastomosing cords of hepatocytes reported in the lamprey (Bengelsdorf and Elias 1950) and trout (Simon et al. 1967) is identical to the pattern of cellular arrangement within the liver of largemouth bass.

Vacuolation of hepatocytes, a common finding in the Bouin's fixed, paraffin embedded tissue of this report has been observed in other species (Ito et al. 1961; Simon et al. 1967; Judd and Cross 1966). Although some investigators (Wood and Larson 1961; Nigrelli and Jakowska 1961) have regarded vacuolation as evidence of fatty degeneration, we were unable to demonstrate sufficient lipid to account for the extreme vacuolation. After our electron microscopic study revealed intensive deposition of glycogen in hepatocytes, we attempted staining of glycogen in thick sections of epon embedded tissue previously fixed in glutaraldehyde. The result was intensive staining for glycogen with little or no vacuolation. These results were similar to those reported in identically processed trout liver (Scarpelli 1967). The problem of glycogen fixation was investigated recently by Leske and Mayersbach (1969). They found that fixatives often recommended for glycogen do not render glycogen irreversibly insoluble, thus histochemical demonstration of glycogen in chemically fixed tissue blocks may not reflect the amount or distribution of glycogen in tissue and cells.

To our knowledge hepatic connective tissue has received little attention in chronic studies of aquatic toxins. The regular, repeating pattern of reticular fibers is often irreversibly altered in aging mice and in those exposed to chlorinated hydrocarbons such as carbon tetrachloride (Hinton and Williams 1968; Popper et al. 1961). Such connective tissue alteration, when caused by hepatotoxins of the aquatic environment, could serve as a functional index of water quality particularly in relation to heavy metals and chlorinated hydrocarbon pesticides.

The amorphous, PAS positive material seen in veins and perivenous spaces of many sections in this study, resembles closely the material described by others (Cope et al. 1970) in the bluegill following chronic exposure to the herbicide 2, 4-D. Although the above report indicated this material to be a pathologic alteration caused by the organochlorine herbicide, we cannot agree for we have seen this material in the majority of our control fish unexposed to any organochlorines. The constant association of this material with blood cells and vessels leads us to assume that we are staining plasma proteins. Albumin and globulin stain positively with the PAS reaction (Pearse 1968).

Glucose-6-phosphatase has been localized within the smooth endoplasmic reticulum of hepatocytes (Chiquoine 1953) and our data concur with the previous observation. When rats were exposed to dieldrin, the initial ultrastructural alteration was hypertrophy of smooth endoplasmic reticulum (Hutterer et al. 1968). If the same alterations occur within fishes exposed to sublethal amounts of aquatic toxins, then the glucose-6-phosphatase reaction may prove extremely valuable as an early indicator of cellular toxicity. Studies are currently underway in our laboratory to investigate this possibility.

Our observations indicate the need for further histopathologic examination into the histochemical/cytochemical effects of aquatic toxins.

Acknowledgments

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The American Eel (*Anguilla rostrata*) in Eastern Lake Ontario[1]

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HURLEY, D. A. 1972. The American eel (*Anguilla rostrata*) in eastern Lake Ontario. J. Fish. Res. Bd. Canada 29: 535–543.

The life history of eels in Lake Ontario was studied by measuring, tagging, and releasing about 1500 individuals between 1958 and 1966. The smallest eels captured were from 295 to 318 mm long. Presumably they entered the lake at about age III–IV at lengths of 200–300 mm. Otoliths of eels from the lake showed a range in age between IV and XVIII, while those of smaller eels from the Ottawa River ranged between age II and IX. The length–weight regressions showed two distinct growth phases: one from about 480 mm to 790 mm, the other from about 830 mm to 1080 mm. Growth of the orbital diameter, interorbital distance, and pectoral fin length in relation to total length was not obviously related to sexual maturity. Eels that emigrated from the lake had a greater weight–length ratio than those that remained in the lake for another year. Of 917 tagged eels transplanted within Lake Ontario, 28 were recaptured near and 18 recaptured far from the original capture site. Although the results are inconclusive, there is a suggestion that eels have home territories within the lake.

HURLEY, D. A. 1972. The American eel (*Anguilla rostrata*) in eastern Lake Ontario. J. Fish. Res. Bd. Canada 29: 535–543.

Dans le but d'étudier le cycle biologique des anguilles du lac Ontario, l'auteur a mesuré, marqué et relâché 1500 poissons au cours des années 1958 à 1966. Les plus petites anguilles mesuraient de 295 à 318 mm de longueur. On présume qu'elles avaient pénétré dans le lac à l'âge III ou IV alors qu'elles mesuraient de 200 à 300 mm. Les otolithes des anguilles du lac révèlent une gamme d'âges de IV à XVIII, alors que celles des anguilles plus petites de la rivière Outaouais marquent un intervalle de II à IX. Les régressions longueur–poids démontrent deux phases de croissance distinctes: une d'environ 480 à 790 mm, l'autre d'environ 830 à 1080 mm. Il n'y a pas de relation évidente entre l'accroissement du diamètre de l'orbite, de la distance interorbitale et de la longueur de la nageoire pectorale d'une part et la maturité sexuelle de l'autre. Les anguilles qui ont quitté le lac ont un rapport poids–longueur plus élevé que celles qui sont demeurées dans le lac une année de plus. Sur un total de 917 anguilles marquées et relâchées dans le lac Ontario, 28 ont été reprises près, et 18 loin de l'endroit de première capture. Bien que les résultats ne soient pas conclusifs, on croit que les anguilles maintiennent dans le lac des territoires propres.

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A long-term investigation of the American eel in Lake Ontario was begun in 1958, first to study the effects of the Robert H. Saunders power dam in the upper St. Lawrence River (Fig. 1) on their migration, and second, to study the life history and population dynamics of this important fish species. This report deals mainly with growth and local movements of eels within the lake during the period 1958–66.

Eels were captured by various types of gear at several locations in eastern Lake Ontario and the Ottawa River. In addition to length and weight, their orbital diameter, interorbital distance, and pectoral fin length were measured. After tagging, they were released at several different locations along the lakeshore. The lengths and weights of eels from both Lake Ontario and the Ottawa River were used to describe the size distribution of eels from these areas, and the length–weight relation of Lake Ontario eels was determined. Otoliths from samples of the catches were used to determine the age and estimate the growth of the fish. Changes in morphometric measurements were related to the size of the eels in an attempt to predict approaching sexual maturity and emigration from the lake. Recaptured

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eels from the lower St. Lawrence River provided data on the size at which eels emigrate, and those from eastern Lake Ontario provided data on local movements within the lake.

Materials and Methods

Source of Animals

The majority of the eels (Table 1) were taken from Prince Edward Bay, which lies on the north-east shoreline of Lake Ontario in Prince Edward County (Fig. 1). Some eels were taken from the Moira River and Hay Bay in the Bay of Quinte (Fig. 1). Because there was no significant difference in the growth rates of eels from these two areas, data from the two groups were pooled.

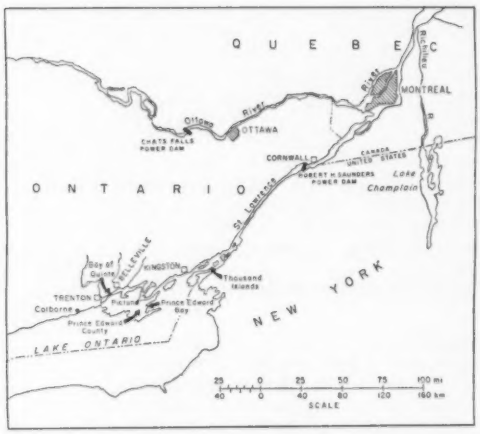

FIG. 1. Map showing some locations mentioned in this paper.

Samples of newly arrived young eels were not obtained from Lake Ontario because they could not be captured with the gear available. In order to have young eels to examine, samples of upstream migrants were taken at the Ontario Hydro dam at Chats Falls on the Ottawa River (Fig. 1) in 1963 and 1964. A 30-ft seine made of nylon flyscreen was held in the current to act as a trap, and eels were swept into it from the apron of the dam. These small eels form part of the annual summer migration that moves into the many tributaries of the St. Lawrence River. It was assumed that these eels were representative of those entering Lake Ontario at about the same time of the year.

Tagging and Measuring of Eels

The eels were anaesthetized with M.S. 222, and a split ring tag was inserted through the lower jaw of each eel using a technique devised by Vladykov (1957). The total length of the anaesthetized eels was measured from the anterior projection of the lower jaw to the posterior edge of the middle caudal ray. The total weight was also recorded. The eye diameter, interorbital distance, and pectoral fin length were measured with dividers and the distances read from a metal rule. The eye diameter was measured in the horizontal plane. After eels were tagged and measured, they were released at predetermined locations.

A few of the larger eels were killed and their gonads examined by W. J. Christie (personal communication).

TABLE 1. Years and locations of capture, and gear used to trap eels for tagging. Many of the eels captured but not tagged were measured and their otoliths were removed for age determination.

Year	Location	Type of gear	No. captured	No. tagged and released
1958	Prince Edward Bay	Hoopnet	362	345
1959	Prince Edward Bay	Hoopnet	296	296
1959	Moira River at Belleville	8-ft trapnet	202	202
1960	Prince Edward Bay	Hoopnet	166	66
1961	Prince Edward Bay	Hoopnet	85	44
1962	Prince Edward Bay	Hoopnet	73	39
1962	Indian Point	Hoopnet	69	54
1963	Prince Edward Bay	Hoopnet	74	73
1963	Ottawa River at Chats Falls	Fixed trap (see text)	302[a]	137
1964	Ottawa River at Chats Falls	Fixed trap	592	564
1964	Prince Edward Bay	Hoopnet	99	87
1966	Hay Bay, Bay of Quinte	Bottom trawl	212	212

[a]These eels were held over winter at Glenora. They did not feed well, and some weight loss was observed. For this reason they were not included in the length–weight regression, but were used in the length–pectoral fin length regressions.

All gonads were similar in appearance, and conformed to published descriptions of the ovary as a frilled, ribbon-like structure (Bertin 1956). It was presumed that all of the eels would most likely be females, since males are rarely found far from salt or brackish water (Gray and Andrews 1970). The gonads of many of the smaller eels from the Ottawa River were probably not differentiated at the time of their capture, since Gray and Andrews (1970) could not sex eels smaller than 220 mm, and even some up to 340 mm.

Otoliths were removed from 212 eels (Table 2) that were captured but not tagged and released. The ages of these eels were determined from their otoliths after preparing them using the technique described by Gray and Andrews (1971).

Recapture

Tagged eels were recaptured by commercial fishermen in eastern Lake Ontario, or as seaward migrants in the lower St. Lawrence River below Quebec City. Those recaptured locally were usually taken in the spring and summer months by fishermen using hoopnets or set-lines. Those taken in the St. Lawrence River were captured between mid-September and late October in weirs. In almost every case the tag was returned, sometimes with information of the date of capture and length and weight of the fish.

Size, Age, and Growth of Eels

Length-Frequency Distribution

Over 46% of 1471 eels taken in Lake Ontario and the Bay of Quinte were between 753 mm and 832 mm in length, with the mode at 792 mm and the median at 776 mm (Fig. 2). As both hoopnets and an 8-ft trapnet used to capture most of the eels had stretched mesh of about 2 inches, the samples taken with them would be biased in favor of large individuals. But the bottom trawl used at Hay Bay in 1966 had stretched mesh of only ¾ inch in its codend. The eels caught with it, from 480 mm to 1060 mm, were probably representative of the eels present.

The length-frequency distribution appears to be skewed somewhat to the left. This could be the result of the loss of some large individuals either to the active commercial fishery or by their migration to sea.

The range in sizes of 302 young eels taken at Chats Falls in July 1963 was from 196 mm to 569 mm, with the mode at 267 mm and the median at 318 mm (Fig. 3). For 592 eels taken from the same location and with the same gear in July 1964, the range was from 208 mm to 505 mm, with the mode at 290 mm and the median at 294 mm (Fig. 3).

The presence of relatively large eels in both years at Chats Falls among the upstream migrants possibly means that these individuals had been resident in the area for a year or more. As few small eels were likely to escape from the gear, the modal length may be more representative of the newly arrived eels than is the mean length. Although the size of these small eels may be indicative of the size of newly arrived individuals in Lake Ontario, the difficulty remains that young eels were not collected at the outlet of the lake. Therefore, the size of newly arrived eels entering the lake was not established.

Age-Length Relation

There was a relatively large range of lengths in each age-group of eels from the Ottawa River at Chats Falls and Lake Ontario (Table 2). Some of the variation was due to difficulties in assigning an age to the eels because of the poor condition of some otoliths.

Eels at Chats Falls were considerably smaller than those from Lake Ontario at the same age (Fig. 4). But the fact that the curves for the two locations appear to converge at age II and III strengthens the contention that the yearly migration seen at Chats Falls is a portion of the main migration seen in the upper St. Lawrence River.

Most of the Chats Falls eels were between 250 and 325 mm in length (Fig. 3). Their age-length relation (Fig. 4) indicates that eels of that size range would be from age IV to possibly age VII. The presence of older eels at Chats Falls could have been the result of their displacement upriver with the arrival of numbers of young eels into the river. In addition, blockage by the Chats Falls dam could have held back sufficient numbers each year so that older eels would be concentrated below the dam. It is doubtful, however, that this dam acts as a complete barrier, since many of the pools and damp areas along the sides of the river could be used as bypasses.

The youngest eels taken from Lake Ontario were age IV, and the oldest was age XVIII. Growth rate was practically linear between age IV and age XIV, but slowed substantially among older eels (Fig. 4). The regression of length on age for eels over the linear portion of the curve from age IV to age XIV was calculated to be: length (mm) = 54.94 age + 112.83.

The age-length relation for Lake Ontario eels was similar to that for Newfoundland eels studied by Gray and Andrews (1971). But Lake Ontario eels remain in fresh water about 7 or 8 years longer than Newfoundland eels, and thus grow to be larger. The age-weight relations, however, showed that Lake Ontario eels were usually heavier at each age than Newfoundland eels.

TABLE 2. Growth in length in relation to age of American eels from the Ottawa River and Lake Ontario.

	Age-group								
	II	III	IV	V	VI	VII	VIII	IX	
				Ottawa River at Chats Falls					
Mean length (*mm*)	197.3	211.8	255.3	289.6	275.6	337.8	386.1	330.2	
SD (*mm*)	5.87	11.01	44.90	–	80.82	61.06	–	–	
Range (*mm*)	190.5	200.7	223.5		218.4	294.6			
	–200.7	–226.1	–287.0		–332.7	–381.0			
No. specimens	3	5	2	1	2	2	1	1	
				Lake Ontario					
Mean length (*mm*)	–	–	309.9	–	508.6	495.3	531.9	532.1	
SD (*mm*)	–	–	13.20	–	126.70	98.06	85.01	123.13	
Range (*mm*)			294.6		406.4	363.2	444.5	368.3	
			–317.5		–673.1	–673.1	–698.5	–739.1	
No. specimens	–	–	3	–	4	10	12	10	
Age-group	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
Mean length (*mm*)	655.2	784.6	786.6	834.6	853.7	909.1	920.0	968.6	909.3
SD (*mm*)	130.19	63.81	79.69	85.04	51.10	71.67	91.71	15.52	–
Range (*mm*)	439.4	629.9	673.1	683.3	779.8	777.2	774.7	955.0	
	–856.0	–899.2	–942.3	–977.9	–965.2	–1043.9	–998.2	–985.5	
No. specimens	27	25	27	33	23	12	5	3	1

Length–Weight Relation

The slope of the regression for all Lake Ontario eels that measured between 483 and 792 mm was 3.77 (Fig. 5). Their growth was allometric since the slope was greater than three. On the other hand, the slope for large eels between 832 and 1076 mm was 2.98, and their growth was symmetric. The slopes of those two lines were significantly different at $P = 0.05$ ($t = 2.88$, df = 13).

Some of this change in slope may have been a consequence of some of the heavier eels having already migrated out of the lake. Data presented later show that eels that are due to migrate in the current season are fatter than eels that will remain in the lake. Vladykov (1955) has described a similar increase in fatness which occurs in the "bronze stage," which he defined as the stage when adult eels descend to the sea. The selective loss of these large, fat eels would have decreased the slope of the length–weight regression.

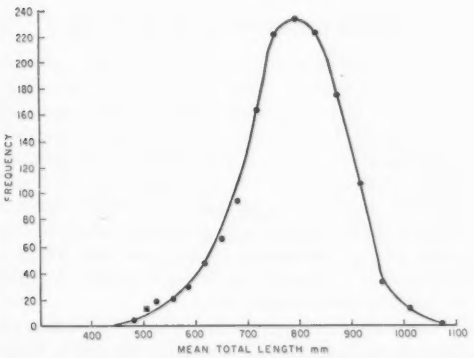

Fig. 2. Length–frequency distribution of 1471 eels from eastern Lake Ontario from 1958 through 1966. Curve was fitted by eye.

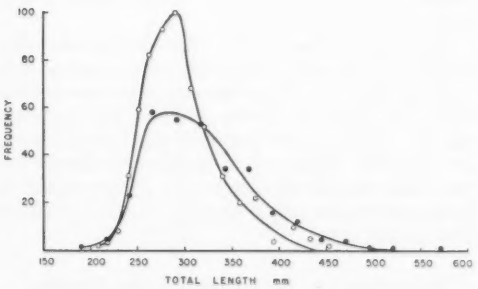

Fig. 3. Length–frequency distributions of 302 eels from the Ottawa River at Chats Falls, July 1963, (closed circles) and 592 eels from the same location in July 1964 (open circles). Curves were fitted by eye.

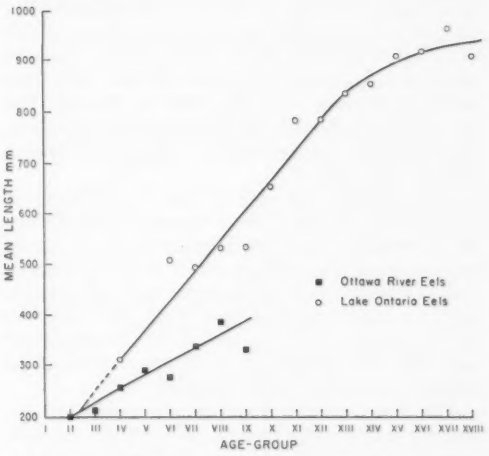

Fig. 4. Mean lengths of eels from eastern Lake Ontario and the Ottawa River at Chats Falls for each age-group.

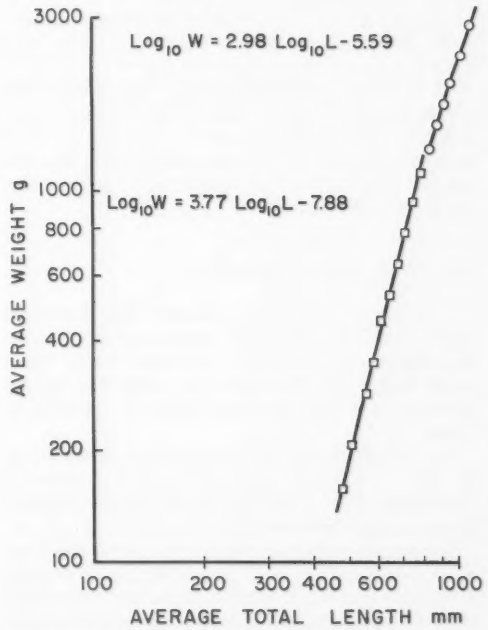

Fig. 5. Length–weight regression lines for Lake Ontario eels grouped into length-class intervals of 22 mm, Equations were calculated by the least squares method. and the lines fitted by eye.

These large eels were still actively feeding at the time they were captured, and thus were not entirely camparable to "bronze" eels, which Vladykov states have ceased feeding. The intensive setline fishery in this area catches a significant number of eels in this size range on baited hooks. Fish of this size have often been captured in trapnets, and they have been obviously feeding on alewife while in the nets. The decrease in the slope of the length–weight regression, therefore, was not the result of cessation of feeding among these eels.

It is possible that part of this change in slope could have resulted from a change in life history that preceeded seaward migration. Frost (1945) noted a significant drop in the slope of the length–weight regression among European eels just prior to their seaward migration. But Gray and Andrews (1971) did not observe a similar shift among silver eels that they examined in Newfoundland. This difference remains to be resolved.

The slope of the length–weight regression for smaller eels in Lake Ontario is much greater than that reported by Gray and Andrews (1971) for Newfoundland eels. They reported the length–weight regression for eels between 159 and 840 mm in one river to be log W = −3.1797 + 3.2706 log L. All but one of the fish were female. In another river, the eels were between 291 and 571 mm, and the length–weight regression was log W = −2.8955 + 3.0812 log L. All of these eels were female. The greater productivity of Lake Ontario water compared to the smaller brooks in Newfoundland is probably one of the factors responsible for the greater weight-for-length increment observed for Lake Ontario eels.

Size At Seaward Migration

Only 36 of 1418 Lake Ontario eels that were tagged and released were recaptured as seaward migrants in the lower St. Lawrence River. Since many recaptured eels were not measured by the fishermen, no data on them could be included in Table 3.

The average length of recaptured eels in the lower St. Lawrence River ranged between 832 and 918 mm (Table 3). According to Fig. 4, eels of this length would be age XIII or XIV.

The average weight of recaptured eels ranged from 1270 to 1614 g (Table 3). The difference in average weight between eels that migrated in less than a year (1631 g) and those that did not migrate for another year (1160 g) was substantial, and indicated that a significant increase in body weight had occurred in the few months prior to migration. The selective loss from the population of some of these heavier eels may be partly responsible for the decreased slope of the length–weight regression seen in Fig. 5 for eels over 830 mm.

TABLE 3. Average lengths and weights of eels at release and at recapture as seaward migrants in the lower St. Lawrence River. Numbers of eels are shown in brackets.

Years between release and recapture	Avg. length (*mm*)		Avg. weight (*g*)	
	At release	At recapture	At release	At recapture
0	874.3(5)	917.7	1630.9(7)	1566.5
1	810.2(5)	857.5	1160.3(5)	1270.1
2	783.6(4)	831.8	966.1(3)	1564.9
3	730.2(2)	838.2	675.8(2)	1360.4
4	746.8(2)	863.6	947.7(4)	1614.0

Relative Growth of Body Parts

In the largest eels taken in Lake Ontario, no evidence was found of enlarged eyes, in contrast to other reports on eels just prior to their seaward migration: by Vladykov (1970) concerning "bronze" eels in New Brunswick and by Boëtius and Boëtius (1967) concerning "silver" European eels. For 683 Lake Ontario eels, the regression of orbital diameter on total body length, calculated by weighted regression (Steel and Torrie 1960), was linear (Fig. 6), the equation being: orbital diameter (mm) = 1.242 + 0.00968 total length (mm).

Practically all of the eels from Lake Ontario were "blunt-nosed" (Bertin 1956), the snout being blunt and somewhat depressed and the eye and nostrils wider apart than in "sharp-nosed" eels. The weighted regression of interorbital distance on body length was linear (Fig. 6). The equation is: interorbital distance (mm) = −2.017 + 0.0250 total length (mm).

Nor was evidence found that the pectoral fins elongate in large eels that are approaching emigration from the lake and sexual maturity. This was in contrast to the report by Bertin (1956) on the European eel. For 527 eels from Chats Falls and Lake Ontario, the weighted regression of pectoral fin length on total body length was linear (Fig. 7), the equation being: pectoral fin length (mm) = −2.883 + 0.0470 total length (mm).

Movement of Eels within Lake Ontario

Eels were captured, tagged, and released at various locations to determine their ability to find their original area of capture. In 1958, 1959,

1960, and 1963, a total of 781 eels were captured at South Bay, taken to Glenora, tagged, and released from there. The numbers of tagged eels that were recaptured over the next few years, and the locations of recapture (Fig. 8), were as follows:

In Prince Edward Bay		Near release point	Outside of Prince Edward Bay
Inner section	Outer section		
11	8	8	16

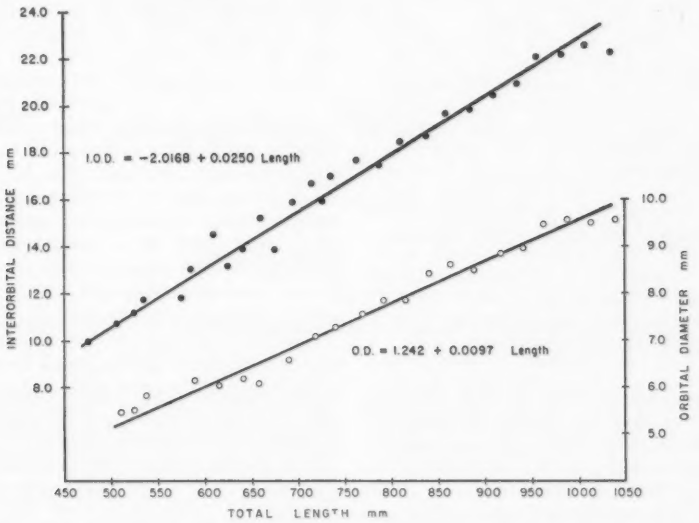

FIG. 6. Regressions of orbital diameter (open circles) and interorbital distance (closed circles) on total body length. Equations were calculated using weighted regression, and lines fitted by eye.

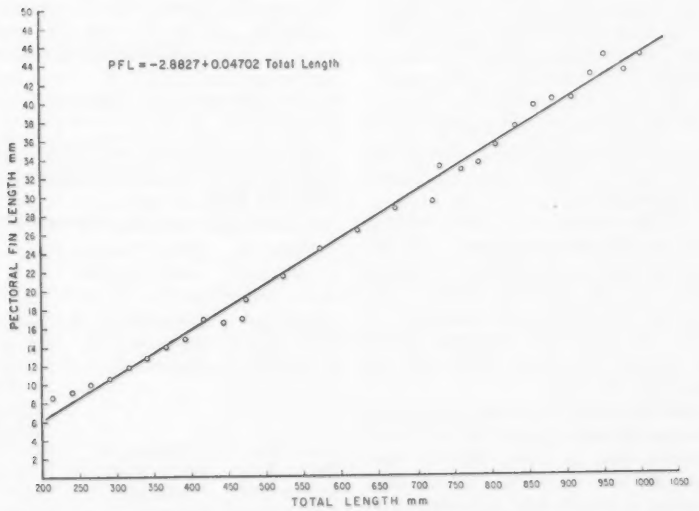

FIG. 7. Regression of pectoral fin length on total body length. Equation was calculated using weighted regression, and line fitted by eye.

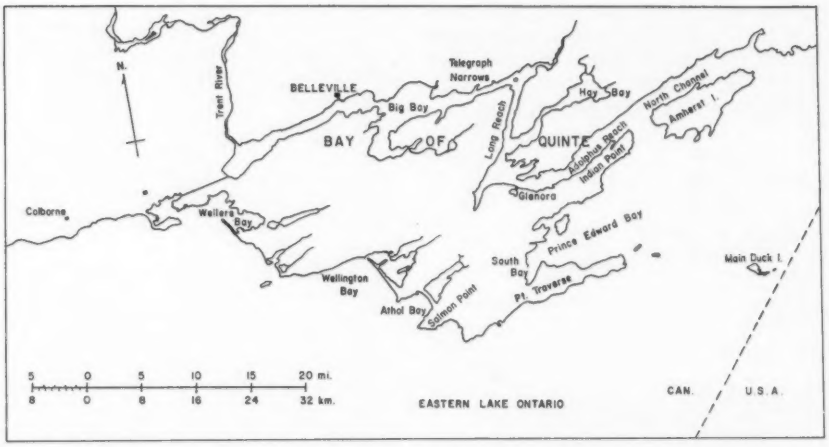

FIG. 8. Map showing locations in Bay of Quinte and eastern Lake Ontario where tagged eels were recaptured in the local eel fishery.

Although the numbers of recaptured eels were rather small, one important constant feature is that the eels were always found either to have returned to eastern Lake Ontario, or to be between the release and capture sites. Those taken near the release point were, in every case but one, recaptured a few weeks following their release. The other eels were recaptured from several weeks to 4 years after their release.

The intensity of commercial fishing for eels in this area was high. For example, in 1958 the weights of eels taken in various sections of the Bay of Quinte and the portion of Lake Ontario near Prince Edward County were: Brighton–Wellers Bay, 11,663 pounds; Point Traverse–Amherst Island, 26,522 pounds; Lower Bay of Quinte–North Channel, 25,387 pounds; Middle Bay of Quinte–Long Reach–Hay Bay–Telegraph Narrows, 8929 pounds; Upper Bay of Quinte, 26,216 pounds.

The level of fishing success was fairly uniform in all areas where the eels were recaptured, with the exception of the middle section of the Bay of Quinte, where lower catches were reported. There is no reason, therefore, to believe that the recaptures in one area were the result of more intensive fishing there compared to any other area where eels are found in eastern Lake Ontario.

In 1962 and 1964, eels from South Bay and Indian Point were cross-transplanted, and some were also released at Glenora and in Lake Ontario near Colborne, about 100 km from the capture sites. Of the 56 eels taken at South Bay and released at Glenora, all five that were recaptured returned to Lake Ontario (Table 4). Three of them were recaptured relatively close to their capture site, one was taken at Indian Point, and another at Main Duck Island in Lake Ontario. Of the 32 eels taken from South Bay and released at Colborne, only one was recaptured, but it was found relatively close to its capture site.

Two of the 37 eels from Indian Point that were released at other locations were recaptured close to their capture site (Table 4). However, one other eel was recaptured in the upper Bay of Quinte, in the opposite direction to its capture site.

Finally, of the 31 eels that were tagged and released at the location of their capture, only one was recaptured (Table 4). It was taken just outside South Bay in Prince Edward Bay.

TABLE 4. Numbers of eels taken at recapture sites in Lake Ontario (Fig. 8) after release at various points in 1962 and 1964.

Point of capture	Point of release and number	Point of recapture and number
South Bay	Indian Point, 11	none recaptured
South Bay	South Bay, 14	Prince Edward Bay, 1
South Bay	Glenora, 56	Prince Edward Bay, 2
		South Bay, 1
		Indian Point, 1
		Main Duck Island, 1
South Bay	Colborne, 32	Point Traverse, 1
Indian Point	Indian Point, 17	none recaptured
Indian Point	South Bay, 21	North Channel, 1
Indian Point	Glenora, 16	Indian Point, 1
		Upper Bay of Quinte, 1

In 1959 and 1966, eels were captured, tagged, and released at the same location. Of 202 eels released in 1959 in the upper Bay of Quinte near Belleville, 17 were recaptured within 16 km of the capture site up to 4 years later. Only one other was recaptured, a large eel (920 mm) taken in the lower Bay a few months after release. In 1966, 212 eels were captured, tagged, and released in Hay Bay, located in the middle portion of the Bay of Quinte. Two of these eels were recaptured there several years later, but none were taken elsewhere.

Although these results indicate that displaced eels tended to return to their original site of capture, they did so with relatively little precision. In addition, it appears that those eels taken in Lake Ontario and released in the Bay of Quinte tended to return to Lake Ontario, while those taken from and released in the Bay of Quinte without exception were recaptured in the Bay of Quinte.

Relatively little is known about the local movements of American eels during their freshwater life. Gunning and Shoop (1962) reported that eels they studied in a Louisiana stream had a maximum home range of only 450 ft. Vladykov (1971) suggests, from some inconclusive experiments on transplanted eels in New Brunswick, that homing occurs. More extensive data on movements of transplanted European eels reported by Tesch (1970) and Deelder and Tesch (1970) strongly indicate that these eels returned to their home area, over a distance of more than 200 km. However, the factors responsible for any homing ability that eels have are, as yet, not known.

Acknowledgments

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Postglacial Dispersal of Four Deepwater Fishes on the Basis of New Distribution Records in Eastern Ontario and Western Quebec

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DADSWELL, M. J. 1972. Postglacial dispersal of four deepwater fishes on the basis of new distribution records in eastern Ontario and western Quebec. J. Fish. Res. Bd. Canada 29: 545–553.

Occurrences in 130 new localities in eastern Ontario and western Quebec are given for the fishes *Cottus ricei*, *Myoxocephalus quadricornis*, *Pungitius pungitius*, and *Percopsis omiscomaycus*. A total of 189 localities for these fishes is now known within this area. The distributions of these species are closely associated with the maximum extent of the large, interconnected, Wisconsin glacial lakes, their outlet channels, and areas inundated by postglacial marine waters. Although all four fishes dispersed primarily by means of the proglacial waters between 17,000 and 6000 years ago, *C. ricei*, *P. pungitius*, and *Percopsis omiscomaycus* have dispersed short distances beyond the glacial lake–marine boundaries and are probably still dispersing as drainage systems adjust themselves to postglacial rebound. Dispersal was probably north and eastward from a Mississippian refugium.

DADSWELL, M. J. 1972. Postglacial dispersal of four deepwater fishes on the basis of new distribution records in eastern Ontario and western Quebec. J. Fish. Res. Bd. Canada 29: 545–553.

La présence de *Cottus ricei*, *Myoxocephalus quadricornis*, *Pungitius pungitius*, et *Percopsis omiscomaycus* a été constatée dans 189 localités de l'est de l'Ontario et de L'ouest du Québec. De ces observations 130 sont nouvelles. La distribution de ces poissons coincide avec l'étendue maximum du grand système des lacs glaciaires apparus après l'âge Wisconsin, de leurs décharges et des régions inondées par les eaux mer grossies par la fonte des glaciers. Bien que la dissémination de ces poissons se fasse probablement surtout par les lacs d'origine glaciaire il y a 6000–17,000 années, *C. ricei*, *P. pungitius*, et *Percopsis omiscomaycus* ont également tendance à se disséminer un peu en amont de leurs limites. La dissemination était probablement vers le nord et vers l'est à partir du refugium du Mississippi.

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THE distribution and biology of many fishes in eastern Canada, particularly those occurring in deep water, are poorly known. This factor has prevented a complete discussion of their zoogeography in the few broad geographic studies (Radforth 1944; Legendre 1953; Scott 1967) that have been done.

During a study of the distributions of glacial relict crustaceans in eastern Canada, *Cottus ricei* (spoonhead sculpin), *Myoxocephalus quadricornis* (fourhorn sculpin), *Pungitius pungitius* (ninespine stickleback), and *Percopsis omiscomaycus* (trout-perch) were frequently captured. In eastern Ontario and western Quebec, these fishes were previously known largely from the Great Lakes, James Bay, and a few widely scattered lakes (Martin and Chapman 1965; Magnin 1965; Delisle and Van Vliet 1968). This paper presents new records that close some of the gaps in the literature on the distributions of these four fishes, thereby allowing discussion of their postglacial dispersal routes.

The glacial lakes and marine transgressions shown in the study area (Fig. 1) are the maximum extents of all glacial waters during retreat of late Wisconsin ice and, with some modifications by the author, are basically those of Prest et al. (1968) and Boissoneau (1968). The presence of a glacial lake in the Gatineau Valley, Que., (Fig. 1 and 3) that is here named glacial Lake Gatineau, was noted by Antevs (1928); its boundaries are given tentatively on the basis of distributions of the relict crustaceans (M. J. Dadswell unpublished data). These glacial lakes did not occur synchronically, but rather in sequence from south to north 17,000–6000 years ago (Prest 1970).

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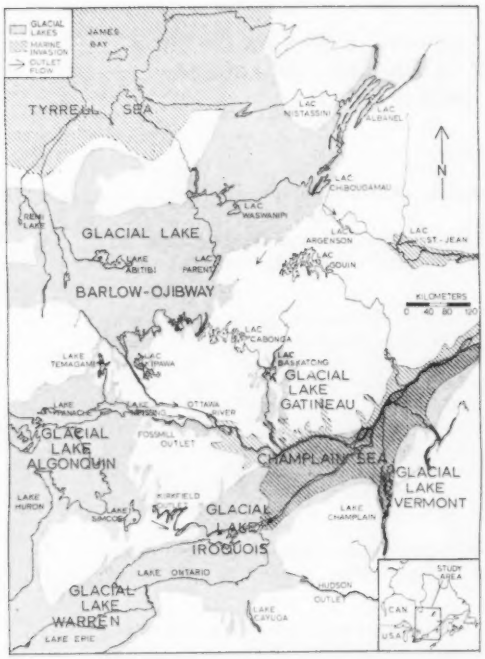

FIG. 1. Maximum extent of the late Wisconsin glacial lakes and marine transgressions (adapted from Prest et al 1968; Boissoneau 1968) in the study area. Glacial Lake Fort Anne and glacial Lake Iroquois joined to form glacial Lake Frontenac and occupied the St. Lawrence lowlands prior to the Champlain Sea transgression (Prest 1970).

Materials and Methods

As the major study was concerned with distributions of relict crustaceans, the sampling methods were directed towards their capture. The main sampling gear was a small otter trawl, 3.5 m across the footrope and 5.5 m long. Mesh size was 38 mm throughout, with an inner 2-m bag of 3-mm mesh in the codend. The trawl was towed along the bottom with a ratio of tow rope to depth of 3:1, at speeds from ½ to 3 kph. Fishing depths were determined using an electronic depth sounder.

In each lake the vertical distributions of temperature and oxygen were first determined, and from these the best trawling depth for the capture of crustaceans selected. Two slow-speed tows of 5–7 min duration were then made at the selected depth, usually 20–50 m. If time permitted, tows were made in shallower water, or deeper water, or both, expressly to capture fish. All trawling was done during daylight.

In all, 372 lakes were sampled with the otter trawl. In 20 of the lakes a 5-m minnow seine was used over sandy beaches after nightfall to obtain trout-perch.

Series of the fish specimens from all localities have been deposited at the National Museum of Natural Sciences, Ottawa, and the Royal Ontario Museum, Toronto.

Distributions Records

A total of 130 new localities were obtained for the four species. One or more of these fishes were found in 101 (53%) of the 191 sampled lakes considered to be within the glacial lake–marine boundaries (Fig. 2 and 3). On the other hand, one or more were taken in only 29 (15%) of the 181 lakes sampled that were considered to be outside the boundaries (Fig. 2 and 3). Furthermore, 84% of the 189 known localities for these fishes in eastern Ontario and western Quebec are within the glacial lake–marine boundaries (Table 1; Fig. 2 and 3). Of 69 lakes in areas inundated only by the maximum levels of the glacial lakes, 51 (75%) were found to contain one or more of these fishes. In only a few instances were any of the fishes found more than 5–10 m above, or more than a few kilometers beyond, the limits of glacial waters. The maximum distance of dispersal upstream to lakes so far known from this study is 60 km, and the maximum known elevation above maximum glacial lake level reached by these fishes is 36 m (Lac Cabonga, no. 63 Fig. 2). In regions where considerable dispersal beyond the glacial lake–marine boundaries has occurred, either the topography is low or the streams are slow and meander through sand plains.

Cottus ricei was the most commonly captured fish and was found in 88 new localities (Table 1). This brings to 100 the known localities for this fish within the study area (Fig. 4). The new localities extend the known distribution of *C. ricei* 700 km eastward in Canada to the northern end of Lac Mistassini. This species is now known to occur in Lake Abitibi; Dymond and Hart (1927) recorded it only from a tributary of the lake.

Although I did no collecting in rivers, there are only two known captures of *C. ricei* from running water in the study area, and in southeastern Canada this fish appears to be predominantly lacustrine. In western Canada this species is commonly found in rivers (McPhail and Lindsey 1970). This apparent difference in habitat may be due to a lack of sampling with an otter trawl in western lakes, or a lack of knowledge of the fishes in the large rivers flowing into James Bay, or both.

In deep, stratified lakes, *C. ricei* was found at depths of 15–50 m and at temperatures ranging from 8–4 C. In these lakes it was moderately abundant, and an average of 2–4 specimens were taken per trawl run. Some lakes (e.g. Lac des Iles, no. 149

Fig. 3) yielded 35 specimens per tow from depths of 40 m. In the shallow, turbid lakes of the Ontario–Quebec clay belt the species was very abundant (50 or more per tow) at depths of 5–10 m and at temperatures as high as 18 C.

Myoxocephalus quadricornis was taken in only five new localities, and these records bring to 11 the known localities for this fish within the study area (Fig. 4 and Table 1). The known distribution now extends into the basin of glacial Lake Barlow–Ojibway. This species was always found at depths of 25 m or more, the average capture depth being 50 m. As in northwestern Canada (McPhail and Lindsey 1970), all of the lakes where this species was found also contained the crustaceans *Mysis relicta* and *Pontoporeia affinis*. Temperatures where it occurred were always below 8 C, although some of the lakes where it was found (Heney, no. 169; Thirty-one Mile, no. 167 Fig. 3) were not particularly oligotrophic, having both moderate dissolved solids (75 ppm) and low oxygen tensions below 30 m (2 ppm or less).

Myoxocephalus quadricornis appears to be sporadically distributed in eastern Canada, and the lack of records obtained may not simply be a result of incomplete sampling. When this species was

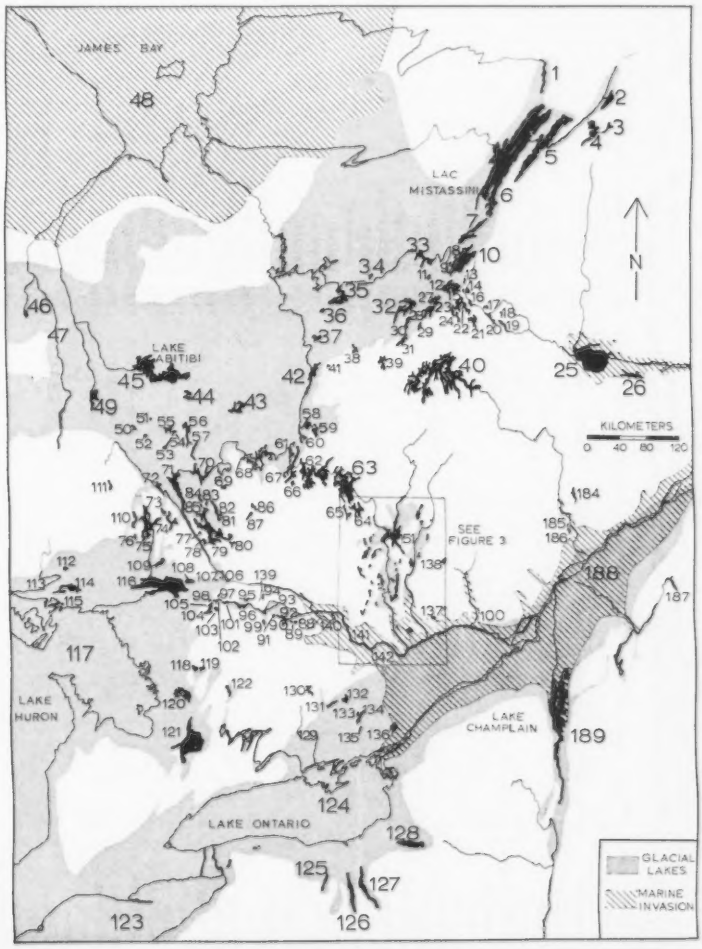

FIG. 2. Localities (solid lakes and numbers) in which one or more of the four species have been found. Numbers refer to localities in Table 1.

TABLE 1. Localities in which one or more of the four deepwater fishes were found. Number of locality indicates position of record in Fig. 2 and 3. Plus sign (+) indicates presence of species. Sources of records are as follows: new records (n. rec.) in this paper; previously unpublished records from Service de la Faune de Quebec (SFQ), Ontario Department of Lands and Forests (ODLF), Royal Ontario Museum (ROM), and the National Museum of Natural Sciences (NMC); previously published records (author's name and date of publication). Unless otherwise specified all localities refer to lakes.

No.	Locality[a]	*C. ricei*	*M. quadricornis*	*P. pungitius*	*P. omiscomaycus*	Source of record
1.	Baudeau	+			+	n. rec.
2.	Bethoulat	+			+	"
3.	Petit Temiscamie				+	"
4.	Temiscamie	+			+	"
5.	Albanel	+		+	+	"
6.	Mistassini	+			+	"
7.	Waconichi			+	+	Richardson (1944)
8.	Gilman			+	+	n. rec.
9.	Caché	+				"
10.	Chibougamau	+		+	+	"
11.	Presqu'île	+		+	+	"
12.	Obatogamau	+			+	"
13.	Dufresne			+		"
14.	Charron				+	"
15.	Malo	+			+	"
16.	Nicabau	+			+	"
17.	Aigremont	+				"
18.	D'Eglis	+				"
19.	Argenson	+				"
20.	Chamouchouane				+	"
21.	Poutrincourt	+			+	"
22.	Rohault	+		+	+	"
23.	Gabriel	+				"
24.	Robert	+			+	"
25.	St.-Jean			+	+	Legendre (1953)
26.	Kenogami			+		SFQ
27.	Caopatrina	+		+		n. rec.
28.	de la Surprise	+				"
29.	Sylvie				+	"
30.	Hébert	+		+	+	"
31.	Lacroix	+			+	"
32.	Doda	+		+		"
33.	Opemisca	+			+	"
34.	Renault	+				"
35.	Waswanipi			+	+	Magnin (1965)
36.	Madelaine	+			+	n. rec.
37.	Quevillon				+	"
38.	Wetetnagami	+			+	"
39.	Mesplet				+	"
40.	Gouin	+				"
41.	Desforges	+				"
42.	Parent				+	"
43.	Preissac	+			+	"
44.	Duparquet	+			+	"
45.	Abitibi	+			+	Dymond & Hart (1927)
97.	Lauder				+	N. V. Martin (pers. comm.)
98.	Boulter				+	"
99.	White Partrige				+	"
100.	Rivière du Nord				+	NMC
101.	Daventry					ROM
102.	Kioshkokwi			+	+	N. V. Martin (pers. comm.)
103.	Threemile				+	"
104.	Waskigomog				+	"
105.	Wilkes				+	"
106.	"Unnamed"				+	ODLF
107.	Kearney			+		ODLF
108.	Trout			+		ODLF
109.	Tomiko	+				n. rec.
110.	Obabika	+				"
111.	Smoothwater				+	ODLF
112.	Fairbank		+			n. rec.
113.	Spanish River				+	ROM
114.	Panache	+				n. rec.
115.	Lumsden				+	Beamish (MS 1970)
116.	Nipissing			+	+	ROM
117.	Huron	+	+	+	+	Hubbs & Lagler (1964)
118.	Vernon	+				ROM
119.	Fairy	+				n. rec.
120.	Muskoka	+				ROM
121.	Simcoe				+	ROM
122.	Twelve-Mile				+	ROM
123.	Erie	+	+		+	Hubbs & Lagler (1964)
124.	Ontario	+	+	+	+	"
125.	Canandaigua			+	+	Greely (1928)
126.	Seneca				+	"
127.	Cayuga				+	"
128.	Oneida				+	"
129.	Moira River				+	NMC
130.	Weslemkoon			+		n. rec.
131.	Kashwakamak			+		n. rec.
132.	Cross	+				"
133.	Crow	+				"
134.	Bobs			+		"
135.	Desert	+				"
136.	Charleston			+		"
137.	Heart			+		"
138.	Nominingue			+		"

47.	Mattagami R.				+	ROM	140.	Hales Creek				+	ROM
48.	James Bay	+	+	+	+	Scott (1967)	141.	Ottawa River				+	Dymond (1939)
49.	Nighthawk				+	n. rec.	142.	Cody Creek				+	NMC
50.	Kenogami	+			+	ROM	143.	Iveteaux	+				n. rec.
51.	Nettie			+		ROM	144.	Chopin	+			+	"
52.	Round	+				n. rec.	145.	Polonais			+	+	"
53.	Wendigo	+			+	"	146.	Tapani	+				"
54.	Raven		+			"	147.	Moreau			+		"
55.	Larder	+			+	"	148.	des Ecorces	+				"
56.	Opasatica	+			+	"	149.	des Iles	+	+	+		"
57.	Remigny	+		+	+	"	150.	Pope	+				"
58.	Gueguen	+			+	"	151.	Baskatong				+	"
59.	Matchi-Manitou	+				"	152.	Serpant			+		"
60.	Villebon				+	"	153.	de la Veille	+				"
61.	Granet	+			+	"	154.	Tomasine	+			+	"
62.	Dozois	+			+	"	155.	Rond	+				"
63.	Cabonga	+		+	+	"	156.	Désert	+				"
64.	Bark	+				"	157.	Bras Coupé	+		+		"
65.	des Loups			+		P. Rubec (pers. comm.)	158.	Lytton	+				"
							159.	Quinn	+				"
66.	Transperant	+				n. rec.	160.	Murray	+				"
67.	Grand Victoria	+			+	"	161.	à l'Achigan			+		"
68.	Nodier				+	"	162.	à la Tortue				+	"
69.	aux Sables				+	"	163.	Pythonga				+	"
70.	des Quinze				+	"	164.	Grand Cèdres	+		+		"
71.	Temiskaming				+	"	165.	Petit Cèdres	+		+		"
72.	Bay	+			+	"	166.	Roddick		+			"
73.	Net	+				"	167.	Thirtyone Mile	+	+	+	+	"
74.	Rabbit	+				"	168.	Pemichangan	+			+	Delisle & Van Vliet (1968)
75.	Temagami				+	ODLF							
76.	Wawiakashki	+			+	n. rec.	169.	Heney	+	+	+	+	"
77.	White			+		"	170.	Danford			+		NMC
78.	Tee	+				"	171.	Bitobi	+		+		n. rec.
79.	Kipawa				+	"	172.	Latourelle			+		"
80.	Booth	+				"	173.	des Iles			+		"
81.	Cooks	+				"	174.	Blue Sea	+		+		"
82.	Ostaboninque				+	"	175.	Profond			+		"
83.	Brisbois				+	"	176.	Paquin	+		+		"
84.	Argentier	+				"	177.	Mer Bleue	+				"
85.	St.-Amand	+		+		"	178.	Cayamant	+		+		"
86.	Sandeau	+				"	179.	Petit Cayamant	+				"
87.	des Loups	+			+	"	180.	Otter				+	"
88.	St. Andrews				+	N. V. Martin (pers. comm.)	181.	Rivière des Aigles				+	NMC
							182.	Priest Creek				+	NMC
89.	Stratton				+	"	183.	MacGregor			+		n. rec.
90.	Carcajou				+	"	184.	Mekinac				+	"
91.	Clemow				+	"	185.	Isaie	+				"
92.	Grand				+	"	186.	la Pêche	+				"
93.	Traverse				+	"	187.	St.-François	+				"
94.	Wendigo				+	"	188.	St. Lawrence R.	+		+	+	Hubbs & Lagler (1964)
95.	Gilmour				+	"							
96.	Cedar	+	+		+	Martin & Chapman (1965)	189.	Champlain				+	"

[a]The geographic positions and altitudes of the localities are available from the author.

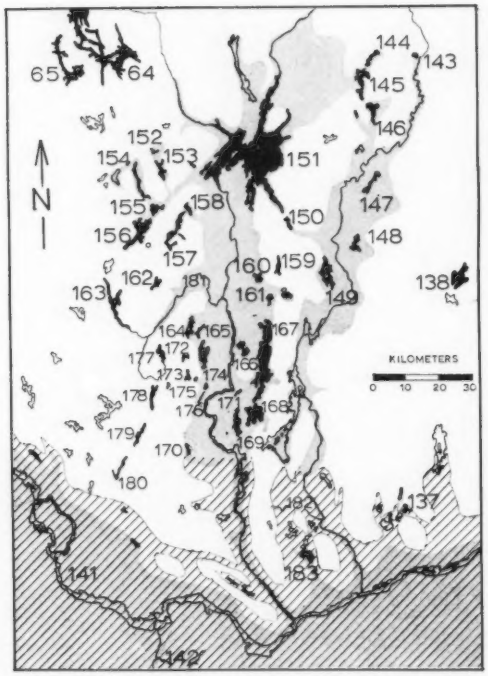

FIG. 3. Maximum extent of the Champlain Sea (cross-hatching; Elson MS 1960) and the later combined Champlain Sea and glacial Lake Gatineau (shading; M. J. Dadswell unpublished data) in the Gatineau Vallee region. Solid lakes were found to contain one of mory of the fishes, open lakes are those sampled in which none of the fishes were found. Numbers refer to localities in Table 1.

found in a lake it was always taken readily and in large numbers. The size of some populations is indicated by the following catch data: Fairbank Lake, 18 per tow; Raven Lake, 15 per tow; Roddick Lake, 33 per tow.

Pungitius pungitius was captured in 36 localities. This brings to 53 the known localities for this fish within the study area (Fig. 4 and Table 1). The known distribution in central Quebec is extended to Lac Albanel.

The ninespine stickleback was usually found in depths from 5–20 m; this agrees with depth distributions found by Reckahn (1970) in South Bay, Lake Huron, and Nelson (1968a) in Illinois for this species. Specimens were occasionally caught as deep as 40 m and as shallow as 1 m. *Pungitius pungitius* was especially abundant in lakes with much submerged aquatic vegetation (Kaswakamak, no. 75; 70 per tow). Catches of this species in 10–30 m of water usually consisted of 2–5 fish per tow.

Percopsis omiscomaycus was collected from 58 new localities. This brings to 108 the known localities for this fish within the study area. *Percopsis omiscomaycus* was found in shallower water than the other three species. The average depth range was 5–15 m, although the fish was captured at 20 m and was commonly taken with a seine over beaches at night if water temperatures were not higher than 21 C. Therefore, during the summer in southern Canada it would be restricted to depths in or below a thermocline, and it is for this reason that I consider it a deepwater fish. Sixty specimens were taken in one tow in Nighthawk Lake (no. 49 Fig. 2); but the average trawl catch in most lakes was 10.

Postglacial Dispersal

The distribution of these four fish species in southeastern Canada suggests that the major routes of dispersal following deglaciation were the interconnecting standing bodies of proglacial waters and their outlets. Their occurrence in 75% of the lakes in areas covered only by the maximum levels of proglacial waters indicates that dispersal closely followed the ice retreat. In support of this hypothesis, it can be stated that all four species are essentially coldwater, lacustrine forms with a limited ability to move upstream. In the ensuing discussion, names and sequences of glacial lakes are greatly simplified from the more complete discussion by Prest (1970).

Current evidence indicates that during Wisconsin glaciation in eastern North America these fishes survived in a Mississippian refugium (Nelson 1968a; McPhail 1963; McPhail and Lindsey 1970). *Pungitius pungitius* and *Percopsis omiscomaycus* are the only two of the four species now known from that area, but *C. ricei* and *M. quadricornis* occur in Lake Michigan just to the north (Hubbs and Lagler 1964).

As Wisconsin ice in eastern North America began retreating approximately 17,000 years ago (Prest 1970), the fishes, following the ice closely, presumably spread first from the Mississippian refugium into glacial lakes Chicago and Warren and thence (Fig. 1) into glacial lakes Algonquin and Iroquois. The Finger Lakes in New York State were probably reached through the connection they had with the late stages of glacial Lake Warren (about 12,500 years ago, Prest 1970).

They probably dispersed into the Muskoka–Haliburton lakes around 11,800 years ago, when glacial Lake Algonquin inundated that region (Prest 1970). Martin and Chapman (1965) have shown that this same means was used by the relict crustaceans to invade the area.

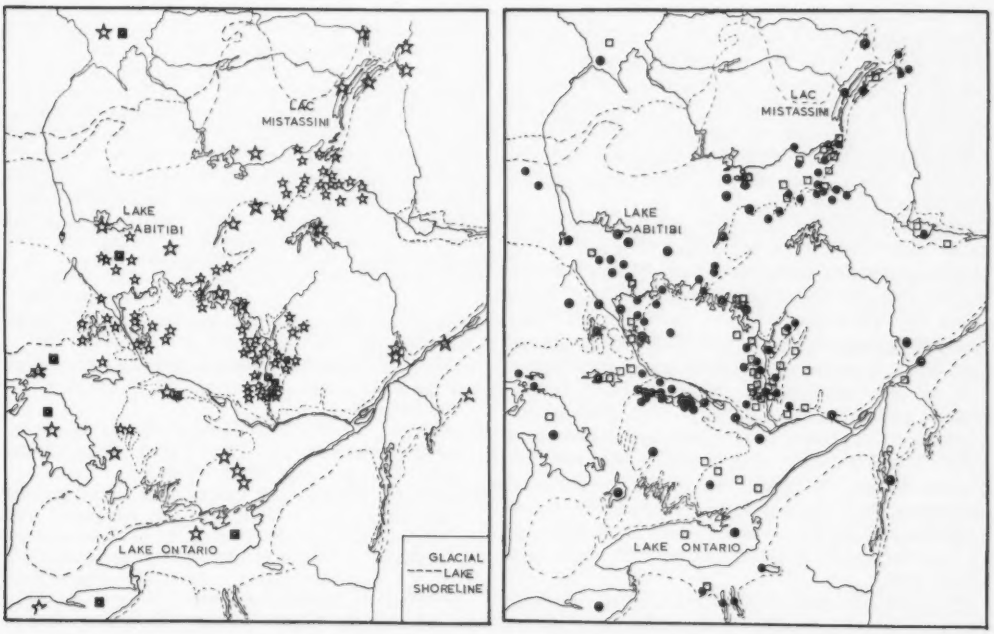

FIG. 4. Known distributions of *Cottus ricei* (stars), *Myoxocephalus quadricornis* (closed squares), *Pungitius pungitius* (open squares), and *Percopsis omiscomaycus* (closed circles) in the study area.

Two routes were available for fishes to disperse into the Lake Champlain area: one down the Hudson Outlet of glacial Lake Iroquois proper (about 12,000 years ago), and the other to the north of the Adirondacks when glacial lakes Iroquois and Fort Anne became connected (Fig. 1) during the Belleville–Fort Anne phase of glacial Lake Frontenac (Prest 1970).

Dispersal into the Ottawa and Gatineau valleys could also have taken place by two routes. Both of these were in existence between 11,500 and 9500 years ago (Prest 1970): one across the Champlain Sea from the south and the other from glacial Lake Algonquin via the Fossmill Outlet (Fig. 1). This latter route has been proposed by Martin and Chapman (1965) to explain the distribution pattern of the relict crustaceans and by Delisle and Van Vliet (1968) to explain the presence of *M. quadricornis* in the Gatineau Valley. The large numbers of records (Fig. 2 and 4) in the Fossmill area for all four species indicate that this route was used extensively for fish dispersal. On the other hand, *Pungitius pungitius* is also present on the Atlantic seaboard and conceivably could have dispersed into the Gatineau from the east as did the smelt (Delisle and Veilleux 1969). This does not seem likely, however, as *P. pungitius* from the Gatineau Valley conforms to McPhail's Mississippian form (1963).

The present day distribution patterns of these fishes, their dispersal abilities, and the limited salinity tolerances of some of them indicate that all four species simultaneously invaded the Gatineau Valley via a brackish or fresh body of standing water. *Percopsis omiscomaycus* apparently has the lowest salinity tolerance of the four species (Nelson 1968b; McAllister 1964; Ryder et al. 1964), but its distribution pattern in the Gatineau Valley is nearly the same as that of the other fishes (Fig. 4), indicating that it dispersed into the Gatineau Valley at about the same time. Due to higher salinity tolerance, *Pungitius pungitius* and *C. ricei* may have been able to invade the area slightly earlier, as indicated by their presence in higher level lakes east of the Gatineau Valley (Fig. 3), which were covered only by more saline stages of the Champlain Sea (Elson MS 1960).

Since the greatest influx of fresh water was probably from the north side of the Champlain Sea (where the glacier was situated) and since dispersal across the sea from southern lakes was probably prevented by high salinities (Elson MS 1960), the probable dispersal route into the Gatineau Valley

was down the Fossmill Outlet and across the northern reaches of the Champlain Sea. The time of dispersal was probably about 10,000 years ago when the Champlain Sea was shoaling and freshening in the northern end (Prest 1970). The distributions of the relict crustaceans in the study area (M. J. Dadswell unpublished data) indicate that a standing body of water linked the Gatineau and Ottawa valleys at this time (Fig. 3).

Dispersal into the Temagami region could have taken place by way of late stages of glacial Lake Algonquin and early stages of glacial Lake Barlow, which alternately flooded this area about 10,000 years ago (Boissoneau 1968). Dispersal into the Barlow–Ojibway basin could have taken place through this same double flooding as well as by way of the Temiskaming reentrant which briefly linked glacial lakes Algonquin and Barlow by standing water around 10,000 years ago (Boissoneau 1968). They probably then dispersed through the various stages of glacial Lake Barlow–Ojibway northwards and eastwards, and reached the maximum limit of the glacial lake system north and east of Lac Mistassini (Fig. 2) about 7500 years ago (Prest 1970).

Considerable short-distance, secondary dispersal of these fishes, excepting *M. quadricornis*, has occurred beyond the glacial lake boundaries, especially along the southern Barlow–Ojibway shoreline (Fig. 2). The additional dispersal in that area may be due to cooler stream temperatures, low topography, and a shifting of Arctic drainage to Atlantic drainage due to isostatic rebound. This isostatic shifting of drainage is especially evident at the headwaters of the Chamouchane River just south of Chibougamau (Fig. 2), and there has been extensive spread of these fishes over the divide in this area.

The distributions of these fishes indicate that their primary means of dispersal in eastern Canada were proglacial lakes and their outlets. Dispersal upstream to lakes has played a secondary role. Most dispersal took place between 17,000 and 6000 years ago, and except in cases of drainage shifts due to isostatic rebound or stream capture, their distributions have remained static since that time.

Acknowledgments

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An Experimental Study of Feeding Behavior and Interaction of Coastal Cutthroat Trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*)[1]

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SCHUTZ, D. C., AND T. G. NORTHCOTE. 1972. An experimental study of feeding behavior and interaction of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). J. Fish. Res. Bd. Canada 29: 555–565.

Feeding behavior of cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*) cohabiting a small coastal lake was studied experimentally to examine the importance of food exploitation as a mechanism for spatial and food segregation observed there. The hypothesis that Dolly Varden could feed more successfully on benthic prey, and cutthroat on surface prey was supported by laboratory experiments involving isolated individuals and interspecies pairs exposed to food in benthic, surface, and both locations. Differences between the species were found in resting and orientation positions and in behavior associated with food searching, location, and capture. Dolly Varden also were more successful than cutthroat in capturing benthic prey at low light intensities. Observed differences in feeding between the species were fully expressed in solitary individuals and did not appear to be magnified by interaction. It is suggested that these differences in sympatric stocks of the two species may be inherent and, therefore, that segregation is largely selective rather than interactive, even though the populations still retain considerable plasticity, enabling them to change diets or habitats when necessary or advantageous.

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Les auteurs ont étudié expérimentalement le comportement alimentaire de la truite cutthroat (*Salmo clarki clarki*) et de la Dolly Varden (*Salvelinus malma*) cohabitant dans un petit lac côtier. Cette étude avait pour but d'évaluer l'importance de l'exploitation de la nourriture comme mécanisme de ségrégation spatiale et alimentaire observée dans ce lac. L'hypothèse que la Dolly Varden exploite avec plus de succès les proies benthiques, et la truite cutthroat, les proies de surface, a été confirmée par des expériences de laboratoire impliquant des individus isolés et des couples des deux espèces exposés à de la nourriture localisée au fond, à la surface, ou aux deux endroits. Des différences interspécifiques se sont manifestées dans les positions de repos et d'orientation, et dans le comportement associé à la recherche, au repérage et à la capture de la nourriture. De plus, les Dolly Varden ont mieux réussi que les truites cutthroat à capturer des proies benthiques à de faibles intensités lumineuses. Les différences interspécifiques d'alimentation se réflètent entièrement dans le comportement des individus solitaires et ne semblent pas s'accentuer par interaction. Selon les auteurs, il est possible que ces différences dans les stocks sympatriques des deux espèces soient inhérentes à chacune et que, par conséquent, la ségrégation soit surtout sélective plutôt qu'interactive, même si les populations retiennent encore une grande plasticité qui leur permet de changer de régime ou d'habitat, si la chose est nécessaire ou avantageuse.

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WHEN closely related fishes coexist in the same macrohabitat, for example, a lake or stream, they commonly segregate spatially into more or less discrete microhabitats. Examples have been described by Northcote (1954), Kalleberg (1958), Nilsson (1965), and Hartman (1965). Though it is often easy to demonstrate segregation of coexisting fishes, a more difficult task is to determine the mechanism by which it occurs.

Two types of segregation, interactive and selective, were first recognized by Brian (1956). The former occurs when interaction between the species, involving exploitation, territoriality, fighting for food,

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predation, or other interferences, results in each segregating into different niches (Nilsson 1967); it has been described in detail between brown trout (*Salmo trutta*) and Arctic char (*Salvelinus alpinus*) in Scandinavian lakes (Nilsson 1955, 1960, 1963, 1965). Interactive segregation is most obvious, or is indeed reinforced, in sympatric populations, as demonstrated by Nilsson's studies, but may break down at least partially in allopatric populations. Selective segregation "consists of the selection by instinctive behavior of totally different habitats" (Brian 1956) and, according to Nilsson (1965), is exampled by the cichlids in Lake Nyasa (Fryer 1959). Interactive segregation might then be an intermediate stage, leading, under appropriate circumstances, to a more fixed selective segregation.

Andrusak and Northcote (1970, 1971) have clearly demonstrated segregation in spatial distribution and feeding of cutthroat trout and Dolly Varden cohabiting in coastal British Columbia lakes but have not investigated in detail mechanisms possibly involved in the segregation process. The objective of this study was to examine experimentally the feeding behavior of lake-dwelling and cohabiting cutthroat and Dolly Varden, and so evaluate feeding as a mechanism for segregation; viz, to determine if there were differences in feeding behavior of the two species that might contribute significantly to their segregation.

Materials and Methods

Field observations on spatial distribution and feeding behavior of cutthroat and Dolly Varden were made on Marion Lake from a row boat with the aid of a viewing box and polaroid sun glasses, and by surface swimming with mask and snorkel. This small lake, about 40 km north of Vancouver, B.C., is described by Andrusak and Northcote (1971). Observations were restricted largely to one 100-m section of the lake, parallel to the shore and including depths to 4 m. This region had a gently sloping mud bottom, many rooted aquatic plants, and submerged logs. All observations were made between 0900 and 1500 hr, since shadows from surrounding mountains made location and identification of fish difficult at other times.

Experimental fish were adult coastal cutthroat (17–21 cm long) and Dolly Varden (18–19 cm long), all from Marion Lake except where noted. The cutthroat were typical coastal specimens as described by Carl et al. (1967), but the Dolly Varden differed somewhat from their general description. They had smaller heads and maxillaries than the cutthroat. Furthermore, their mouths were slightly subterminal and their snouts blunt, whereas the cutthroat had distinctly terminal mouths and pointed snouts.

A stock supply of experimental fish was held from early spring to winter, 1968, in two concrete laboratory troughs ($3.7 \times 0.4 \times 0.4$ m) at densities of 20–30 fish per trough and including both species. A slow flow of water was maintained in the troughs, with complete exchange taking about 3 hr. Water temperature ranged from a minimum of 6 C early in the year to a maximum of 14 C in August. Fluorescent overhead lights were controlled by an outside photoelectric cell to approximate a natural photoperiod. Fish were fed daily an excess of food consisting of frozen brine shrimp, frozen fish, and horse heart.

All observations on distribution, feeding behavior, and interaction were made in experimental tanks housed in a separate room where noise and external interferences were negligible. The tanks, $122 \times 61 \times 61$ cm, were made of painted plywood with plexiglass fronts. Three of the four tanks were divided in half by a removable fibreglass screen partition that was used to separate single individuals of each species prior to testing. The fourth was unpartitioned and used as an observation tank for all experiments. Lines on its plexiglass front defined four equal quadrants. Each tank was illuminated by a single "cool white" General Electric fluorescent tube providing approximately 500 lux at the water surface and 240 lux at a depth of 48 cm (8 cm from bottom). All experiments, unless stated otherwise, were conducted under this light condition. A 14-hr day and 10-hr night photoperiod was maintained in the tanks. Black curtains were hung between and above the tanks. Water temperature was similar to that in the holding troughs.

For some experiments, light intensity was varied by replacing the fluorescent lamp with two 60 w "shadow ban" white incandescent bulbs in circuit with a Variac voltage regulator. Light intensities were measured in very approximate lux units with a Photovolt Model 514 M photometer fitted with phototube C and a scotopic (human eye) correction filter. The phototube was housed in an underwater case with an opal diffusing glass and had a reasonably close fit to a cosine response curve. It was calibrated in June 1968, with a N.B.S. foot candle lamp.

Stomachs of the fish were evacuated with a stomach pump similar to that described by Seaburg (1957). It had a 1.5-mm inside diameter copper inlet tube and 6-mm outlet tube. The pump was virtually 100% efficient in recovering chironomid larvae eaten in the preceding hour, on the basis of repeated trials in which larvae in the tank were counted before and after a feeding session. Fish were anesthetized in a .06% solution of 2-phenoxyethanol prior to pumping. No adverse effects from this procedure were evident. Experimental fish in the observation room usually had their stomachs evacuated in the morning if experiments were scheduled for later in the day. This was done in an attempt to standardize hunger levels. No experiments were run until at least an hour after evacuation, although the fish would feed within 5–10 min of recovery from the anesthetic. The stomach pump was also used at the end of each feeding experiment to get a direct count of the number of food items eaten.

Field Observations

Spatial Distribution

Within the 4-m depth zone studied in Marion Lake during 8-hr observation in August and September 1968, no cutthroat but a considerable number of Dolly Varden were observed within a few centimeters of the bottom, as follows:

	0–2-m depth zone		2–4-m depth zone	
	Near bottom	Off bottom	Near bottom	Off bottom
Cutthroat	0	14	0	11
Dolly Varden	0	0	30	48

None were noted on the bottom, perhaps because of the difficulty of seeing immobile fish lying there. Several cutthroat, all near the surface, were observed within the 2-m contour. Both cutthroat and Dolly Varden were seen in midwater areas of the 2–4-m depth zone, but the former were all recorded within the upper 2 m. Cutthroat frequently were "hovering" in the shallows when first seen, but shortly thereafter moved away. Dolly Varden, on the other hand, often could be watched for several minutes before being disturbed. The observed differences in spatial distribution of the two species in the onshore area of the lake agree with gillnet distribution data obtained by Andrusak and Northcote (1971).

Dolly Varden appeared to be more gregarious than cutthroat, often in groups of two or three and occasionally in loose aggregates of five or more.

The numbers seen in the 8-hr observation in August and September 1968, within the 4-m depth contour, were:

	One	Two	Three	Four	Five up
Cutthroat	23	2	0	0	0
Dolly Varden	16	6	6	1	3

None of the cutthroat were in close association with Dolly Varden. These observations agree with gillnet data of Andrusak (MS 1968) which showed that during summer Dolly Varden were highly clumped in the nets, whereas cutthroat were either dispersed or randomly distributed.

Feeding Behavior

Dolly Varden were frequently observed feeding at bottom in the 2–4-m depth zone in Marion Lake. Such individuals swam slowly, more or less parallel to the bottom, but often stopped momentarily as they dipped to pick up and then apparently reject bottom material. Others, mostly small individuals (<15 cm), were observed feeding in midwater, apparently on plankton, as they "mouthed" at small objects with frequent lateral and vertical changes in direction. The locations of those observed in 2 hr on September 5 and 6, 1968, were as shown:

	Cutthroat	Dolly Varden
Bottom	0	13
Midwater	0	12
Surface	3	0
Caught at surface	20	0

Feeding cutthroat were positively identified on a few occasions, and all were capturing insects at the surface. Many other surface-feeding fish were seen too far from the boat to be positively identified; the majority probably were cutthroat. As shown above, only cutthroat were taken when an artificial fly was presented at the surface.

Laboratory Experiments

Spatial Distribution

Cutthroat and Dolly Varden differed considerably in the depth at which they appeared to rest during the day in the observation tanks. Dolly Varden most frequently lay directly on the bottom, occasionally on their bellies but most often supported by the caudal, pelvic, and pectoral fins. In contrast, cutthroat rarely rested on the bottom but usually hovered near one place in the water column. In the holding troughs, where cutthroat and Dolly Varden were together, most of the latter hovered close to or lay on the bottom, but all of the cutthroat hovered off the bottom.

Solitary Feeding

Exposed benthic prey — The ability of solitary fish of each species to locate and capture green chironomid larvae (*Psectrotanypus* sp.) on a leaf-litter and sand substrate at the bottom of the tank was compared in the first series of experiments. Each fish tested had fed previously on this type of larva. Feeding time was held at 10 min and the ration set at 25 larvae. Searching time was recorded for each species, and both prey captured and "bottom grabs" were expressed per unit searching time. Fish were considered to be searching if they remained within 6–7 cm of bottom and appeared to be orienting to it visually. Per unit searching time,

TABLE 1. Feeding attempts and success of solitary cutthroat and Dolly Varden with green *Psectrotanypus* larvae on a sand and leaf-litter substrate.

Species	Bottom grabs		Larvae captured		Minutes spent searching		Bottom grabs per min searching	Captures per min searching
	Mean[a]	Range	Mean[a]	Range	Mean[a]	Range		
Cutthroat 1	2.4	0–5	0	–	1.0	0.5–2.0	2.4	0
Cutthroat 2	18.8	7–28	2.2	0–5	8.6	6.0–9.0	2.2	0.2
Dolly Varden 1	19.2	15–24	2.2	0–5	2.7	1.5–3.5	7.1	0.8
Dolly Varden 2	34.2	12–60	5.8	1–9	6.2	4.0–8.0	5.5	0.9

[a]Mean of five replicates.

Dolly Varden made nearly three times as many bottom grabs and over three times as many captures as the most efficient cutthroat (Table 1). A Mann-Whitney U Test (Siegel 1956) showed these differences to be statistically significant ($P < 0.01$).

There were obvious differences between the species in their pattern of swimming as they searched for chironomid larvae on the substrate. Cutthroat alternated between hovering as they "scanned" the bottom for larvae and cruising slowly not far above the substrate. Dolly Varden cruised almost constantly when searching (Fig. 1), only stopping occasionally when they were "sorting" and rejecting sand and litter from a bottom grab. Usually this process occurred while the fish continued to swim. They searched close to the bottom (within 5 cm), often with pectoral fins brushing the substrate, whereas cutthroat usually scanned the bottom from 5 to 15 cm above it. Both species searched with bodies parallel to or very slightly inclined to the substrate, tilting down only to investigate or pick up objects.

Dolly Varden usually swam more rapidly than cutthroat as they searched for larvae. To quantify this, the speeds of six fish accustomed to tank residence were recorded by timing their movement over 26-cm courses within the tank while searching for 25 red chironomids (*Chironomus* sp.) on sand and leaf-litter substrate. In addition to corroborating the previously observed intermittent swimming behavior of cutthroat in contrast to the more constant swimming of Dolly Varden, the experiments showed that the average searching speed (20 replicates over several days) of the latter species was nearly twice that of cutthroat, as shown: Cutthroat 1, 2, and 3: 2.7, 3.1, and 3.0 cm/sec, respectively; Dolly Varden 1, 2, and 3: 7.1, 5.4, and 5.3 cm/sec, respectively. Differences between species were highly significant ($P < 0.01$).

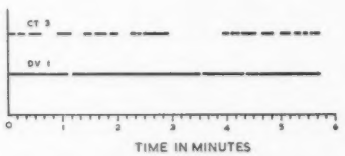

FIG. 1. Typical sequence of searching by a solitary cutthroat (CT 3) and a Dolly Varden (DV 1) for red *Chironomus* larvae on a sand and leaf-litter substrate. Solid lines indicate cruising; breaks indicate hovering. Data obtained with Rustrak event recorder.

Cutthroat and Dolly Varden showed several differences in behavior associated with feeding on chironomids, although both appeared to search visually. Almost invariably, when cutthroat "grabbed" at the bottom they selected a specific object such as a single larva, an evergreen needle, or a stone. Little of the surrounding substrate was picked up when these were taken. Cutthroat often located an object on the bottom, swam over to it, and then moved on without picking it up. Dolly Varden seemed less discriminatory. They picked up and rejected "mouthfuls" of litter and sand, retaining the larvae while expelling the sand from the mouth. Dolly Varden often repeated this with little delay between grabs.

Frequently, cutthroat apparently struck at but missed larvae. To compare "strike success" between the species, about 15 *Chironomus* sp. larvae were scattered over a sand substrate before introducing the fish to the tank. Irregularities in the sand substrate provided some cover for unburied larvae. Each fish was tested on at least three occasions. Cutthroat searched 5–15 cm above the sand and tended to dive down at larvae when sighted, apparently sucking in individuals without picking up much surrounding sand. Consequently, they frequently missed partially buried larvae or those in small depressions (see below). Dolly Varden searched within 5 cm of bottom, scooping up considerable amounts of sand with each larva captured. Misses were rare. Occasionally a larva was expelled with the sand, but was always recaptured immediately.

	Captures	Misses	Strike success (%)
Cutthroat 1	25	12	68
Cutthroat 2	45	9	83
Cutthroat 3	24	13	65
Dolly Varden 1	28	0	100
Dolly Varden 2	24	0	100
Dolly Varden 3	25	2	93
Dolly Varden 4	31	0	100

Buried benthic prey — To test the ability of cutthroat and Dolly Varden to capture prey buried within the substrate, a series of experiments was conducted with tubificid worms. All fish tested were fed *Tubifex* sp. the day before the experiments started. Both species readily consumed the worms. On the first of a 5-day series, *Tubifex* were densely distributed on the bottom of the tank. When most worms had buried themselves thoroughly in the 5-mm deep sand substrate (a few always remained partially or completely exposed), a fish was introduced for a 10-min feeding period. Thereafter it was removed, and ingested *Tubifex* were recovered with the stomach pump. Recovered worms were commonly broken; pieces 10 mm or longer were scored as one worm. Substrate and prey were not disturbed during each series except for addition of more worms on the third day. Predation had little effect on original densities. Four fish (two cutthroat and two Dolly Varden) were tested in random suecession each day as isolated individuals, with results as follows (M, mean; R, range):

	No. trials	Bottom grabs		Worms ingested	
		M	R	M	R
Cutthroat 3	5	25	6–43	4	0–9
Cutthroat 4	5	26	7–48	4	0–15
Dolly Varden 1	5	51	38–60	74	53–115
Dolly Varden 4	5	33	20–50	36	10–65

Cutthroat captured only the few worms that were completely exposed. They picked up little or no sand with each worm, and most of their bottom grabs were at fecal material and bits of plant debris on the sand. On the other hand, Dolly Varden captured many buried *Tubifex* sp. They swam a few centimeters above and parallel to the bottom, then tilted at an angle of 45–60° and scooped with their mouths into the substrate. Most sand grains were expelled from the mouth (occasionally from under the operculars) as worms were sorted from the sand. Sorting of prey from substrate involved a chewing movement that seemed very effective. For example, Dolly Varden 1 captured 53 *Tubifex* the first day tested but had only 20 sand grains amongst them. The same individuals of both species, when tested at the end of the 5-day experiment, found and ate unburied *Tubifex* with similar rapidity in a tank with no sand substrate.

Surface prey — To compare feeding behavior of solitary cutthroat and Dolly Varden at the water surface, experiments were performed in the tank with *Drosophila* adults as prey. A sand substrate covered the bottom, but no benthic food was present. Three cutthroat and two Dolly Varden were used. Each fish was tested once a day for 4 consecutive days. During the previous 60 days these fish had been fed bottom foods only (chironomid larvae and *Tubifex*).

In each experiment, approximately 25 freeze-killed *Drosophila* were clumped on the water surface before the experimental fish was introduced. Once this original ration of flies was consumed, single *Drosophila* were blown gently into the tank through a long air hose, and the time from prey arrival on the surface until capture was recorded, as was the number and duration of "trips" to the bottom by each fish. Immediately after each capture another fly was introduced. This procedure was repeated 15 times.

Cutthroat captured surface prey much more rapidly than did Dolly Varden, especially during the first day (Fig. 2). Cutthroat usually cruised or hovered within 20 cm of the surface for most of the feeding period. Although Dolly Varden swimming near the surface seemed to locate surface prey from about the same distance as did cutthroat, they frequently returned to the substrate and continued "searching" behavior. The frequency and duration of such trips to the bottom decreased over the 4 days tested (Fig. 3), which accounted for the daily increase in their capture rate of surface prey.

Surface and benthic prey — A final series of experiments with solitary fish was conducted using prey available both at the bottom and surface of the tank. Fifty red *Chironomus* larvae were distributed on a sand and leaf-litter substrate as in previous benthic feeding experiments, and 25 live *Drosophila* were scattered on the surface just before introducing the fish. Bottom grabs were recorded, as were the number of times a fish moved into the upper half of the tank (a "surface trip"). "Surface grabs" were scored each time the fish nipped an object floating on the surface.

Cutthroat left bottom once the flies were discovered, cruised back and forth within 15 cm of the surface, and captured all surface prey before returning to search the bottom. Cutthroat made more surface grabs than Dolly Varden (Fig. 4). The

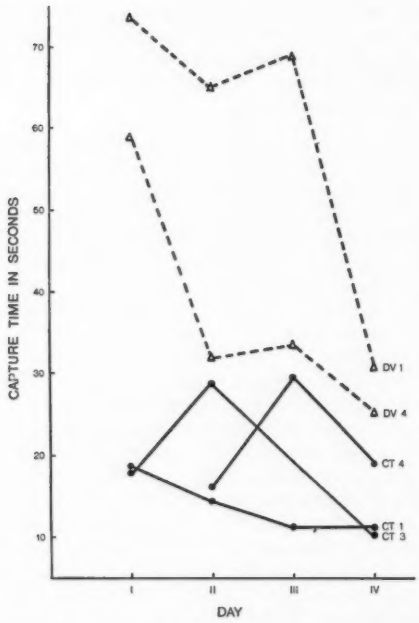

FIG. 2. Average daily capture rates of solitary cutthroat (CT 1, 3, 4) and Dolly Varden (DV 1, 4) feeding on single *Drosophila* adults at the surface.

duration of each of the first few surface trips was long, and after only one or two trips each cutthroat had averaged 20–25 surface grabs.

Dolly Varden did not stay at the surface long. They ranged between surface and bottom, making two to four surface trips every 5 min, capturing one to three flies per trip. After each brief trip to the surface they resumed searching for larvae. This pattern persisted for the full 30-min feeding session, and usually resulted in incomplete exploitation of the surface prey.

INTERACTIVE FEEDING

To study interactive feeding at benthic and surface locations without possible complications of food preferences, experiments were conducted with pairs of similar-sized cutthroat and Dolly Varden exposed to a single food type. Eleven cutthroat and 13 Dolly Varden were used to make up the 18 pairs tested.

The food was frozen trout flesh cut into small pieces about 3 mm^3. During each 3–6-day series, the fish had no food other than that obtained in the experiments. Usually each pair of fish was tested in the morning and evening, but on some days only one test was completed. Tests were repeated five times for each pair. There was no substrate in the tank, but a large boulder at each end provided cover.

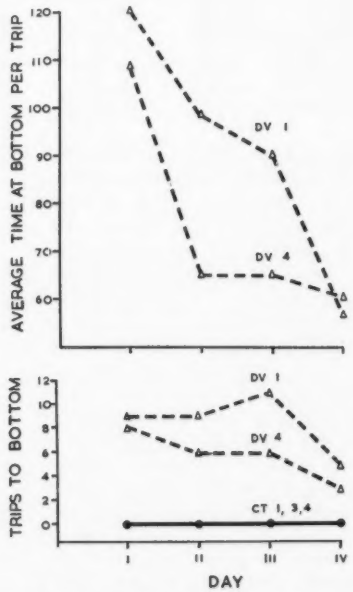

FIG. 3. Number and duration (sec) of "bottom trips" by solitary cutthroat (CT 1, 3, 4) and Dolly Varden (DV 1, 4) during their first four feeding sessions on *Drosophila* adults at the surface.

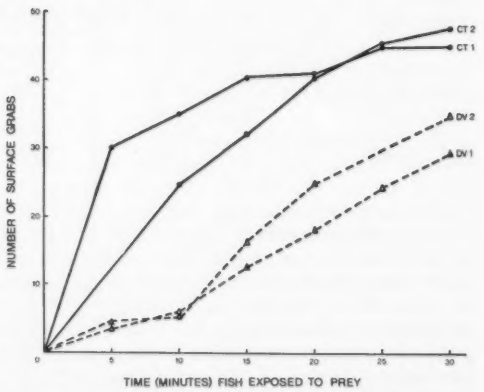

FIG. 4. Cumulative average number of "surface grabs" by solitary cutthroat (CT 1, 2) and Dolly Varden (DV 1, 2) exposed to benthic prey (50 *Chironomus* larvae) and surface prey (25 *Drosophila* adults). Surface prey caught after 30 min: CT 1, 100%; CT 2, 100%; DV 1, 60%; DV 2, 86%.

The cutthroat and Dolly Varden were placed in the tank 24 hr prior to the first test and left there for the duration of the experiment. The plexiglass windows in the tank were covered with half-aluminized plastic film that acted as a one-way mirror. Food was introduced through permanently mounted plastic inlet pipes that protruded from both ends of the tank.

Benthic prey — Twenty pieces of food were individually flushed down the two inlet pipes with water. The food drifted out onto the bottom with no obvious turbulence or bubbles to mark its arrival, and usually the fish found each piece before the next arrived. Considerable aggressive behavior was observed in some pairs, with the result that one fish usually became dominant. The number of aggressive nips was scored for three 10-min periods before, during, and immediately after feeding. These scores were used to classify each fish as the dominant or subordinate of its pair. In pair VIII and X (Fig. 5), the Dolly Varden came from an allopatric coastal population (Dickson Lake).

In three of the seven pairs "scrambling" for bottom food, a cutthroat dominated; no fish was obviously dominant in the other pairs. Dominant cutthroat always got 85% or more of the rat on (Fig. 5). Where dominance did not occur the Dolly Varden fared much better, getting a significantly larger share of the ration in three of the four pairs ($P < 0.05$ using average angular transformeds cores; Steel and Torrie 1960).

Surface prey — In this series of experiments the procedure was the same as with benthic prey, except that food items were introduced at the surface, each making a small disturbance as it entered the water. The Dolly Varden of pair III (Fig. 6) came from an allopatric coastal population (Dickson Lake).

In four of the five pairs cutthroat dominated, never obtaining less than 55% of the ration (Fig. 6). Their mean share was significantly higher than that of the other species. The Dolly Varden was dominant in the fifth pair, but this was not unexpected since it was the only pair used in which there was an appreciable size difference between the two species (cutthroat 128 mm, Dolly Varden 165 mm). Even so, the cutthroat's share of the ration was always close to 50%. Cutthroat appeared to "out-scramble" Dolly Varden as both responded to food introduced at the surface. Frequently there was a race for food, but usually it was won by the cutthroat.

Surface and benthic prey — To provide the possibility for spatial segregation of the fish while feeding, a third series of experiments was run, similar to the previous two, except that food was introduced simultaneously at the bottom and surface of the tank; the 20-item ration was introduced two pieces at a time.

Six pairs of fish were tested; pair XIII (Fig. 7) Dolly Varden was from Dickson Lake. In each case the cutthroat was dominant. As when prey was presented only at the surface, the cutthroat in each pair obtained a much higher percentage of the surface prey than did Dolly Varden (Fig. 7). In at least four of the six pairs, Dolly Varden usually captured more benthic prey than cutthroat, but the difference in mean scores of benthic prey between Dolly Varden and cutthroat was not significant ($P > 0.05$). Nevertheless, Dolly Varden obtained

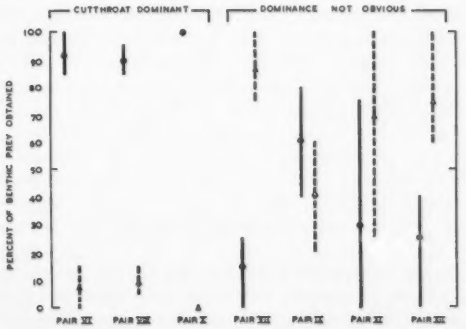

FIG. 5. Capture success of paired cutthroat and Dolly Varden "scrambling" for 20 food items introduced one at a time at bottom. Cutthroat (●), Dolly Varden (△) are averages of five replications; vertical lines give ranges.

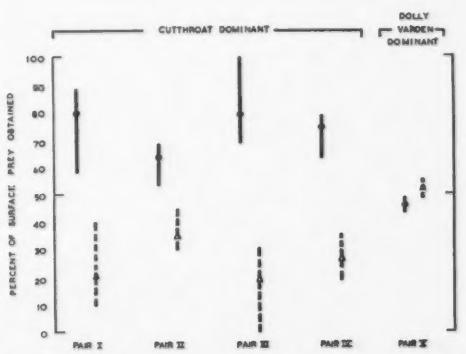

FIG. 6. Capture success of paired cutthroat and Dolly Varden "scrambling" for 20 food items introduced one at a time at the surface. Cutthroat (●), Dolly Varden (△) are averages of five replications; vertical lines give ranges.

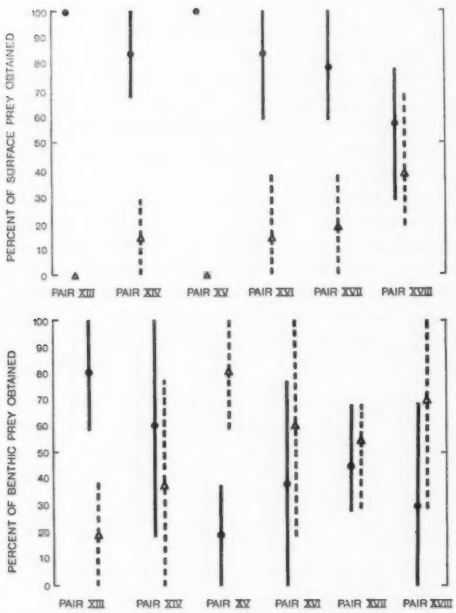

FIG. 7. Capture success of paired cutthroat and Dolly Varden "scrambling" for 20 food items introduced two at a time (one surface, one bottom). Cutthroat (●), Dolly Varden (△) are averages of five replications; vertical lines give ranges; cutthroat dominant in all pairs.

a much higher proportion of benthic food than when only benthic food was available to dominant cutthroat (Fig. 5).

There was, however, no distinct spatial segregation between the species when food was available both on bottom and at surface. Dolly Varden, as usual, spent more time in the lower half of the tank. Cutthroat also spent more time cruising in the lower half. This position was probably advantageous for locating and responding to surface food, which quickly sank. Cutthroat did not actively search bottom, seemed to be more oriented to the surface, and responded quickly to surface food.

Dolly Varden showed a weaker response to surface food but a more vigorous searching behavior on bottom. Use of a deeper tank and floating surface food might have resulted in definite spatial segregation.

LIGHT INTENSITY EFFECTS

To test feeding ability at low light intensities, six solitary fish were given 10-min feeding sessions in the observation tank at four levels of illumination. No individual was tested more than once a day. Prey consisted of 25 red *Chironomus* larvae distributed on the bare tank bottom 10 min prior to introducing the fish. At the highest intensity, cutthroat and Dolly Varden captured approximately equal numbers of larvae (Fig. 8). With the first reduction in intensity, cutthroat caught significantly fewer larvae than did Dolly Varden (Mann-Whitney U Test; $P<0.05$). Although both species showed further decreases at each lower level tested, the effect was much more pronounced in cutthroat. After the long adaptation period (Fig. 8), feeding ability of two of the three cutthroat and all three Dolly Varden increased, but each Dolly Varden captured at least twice as many larvae as the most successful cutthroat.

The "searching" behavior of both species at low light intensities was quite different from that of the highest intensity tested (the latter similar to that described previously). At the lowest level, individuals of both species searched with their snouts almost touching bottom and their bodies tilted at angles of 45° or steeper. Cutthroat no longer hovered and scanned for food, but moved slowly and steadily along bottom when searching. They showed a greater tendency than Dolly Varden to stop searching under these conditions and would

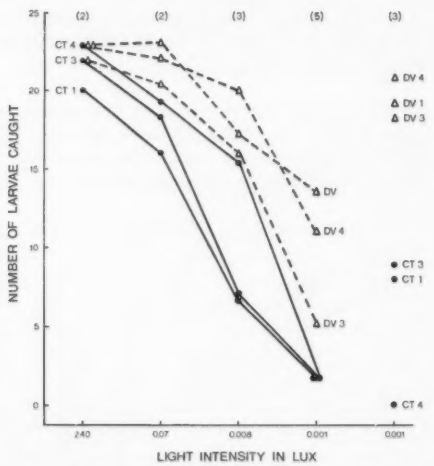

FIG. 8. Effect of light intensity (8 cm above tank bottom) on average number of red *Chironomus* larvae captured by solitary cutthroat (CT 1, 3, 4) and Dolly Varden (DV 1, 3, 4) during a 10-min feeding session. Number of replicates per fish shown in brackets; fish given 10-min dark adaption period for tests at 0.008 and first 0.001 lux light intensity, but 40 min at the final 0.001 lux intensity.

then swim in midwater. Both species appeared to move much slower than at higher intensities.

Discussion

The laboratory experiments reported herein have revealed a number of differences in feeding behavior of solitary cutthroat and Dolly Varden that might provide a means for their segregation when cohabiting in lakes. Feeding habits of each species seemed closely related to their characteristic spatial positioning. A similar relation between spatial distribution and feeding has been suggested in other species. For example, Thomas (1962), in discussing the different foods eaten by juvenile Atlantic salmon and brown trout, speculated that trout fed more heavily on winged insects because they spent more time than salmon in midwater. The salmon more often lay on the bottom and fed predominantly on benthic organisms.

Owing to differences in searching behavior on the bottom observed between the two species, cutthroat may have fewer benthic organisms "available" to them than Dolly Varden. In the laboratory experiments, cutthroat captured only those organisms that were exposed on top of the substrate. The Dolly Varden's ability to feed on buried *Tubifex* indicates that it can prey on both exposed and buried organisms. In Marion Lake, chironomid larvae and *Pisidium* were among the most important foods in the Dolly Varden diet, but made only an insignificant contribution to cutthroat diet (Andrusak and Northcote 1971). This held true even when surface insects were scarce and cutthroat were feeding on bottom.

Cutthroat in the laboratory appeared to be more "surface-oriented" than Dolly Varden, and responded quickly to surface insects after weeks of feeding only on benthic foods. Andrusak and Northcote (1971) indicate that this also occurs in Marion Lake. On the day after the lake became ice-free (following several months ice cover), terrestrial insects made up 10% of cutthroat stomach contents. Dolly Varden stomachs contained none. A week later this food item comprised 86% of total food volume for cutthroat but only 12% for Dolly Varden. This may indicate that cutthroat find and exploit surface food before the other species, or it may reflect a lack of searching at the surface by Dolly Varden even when food is reasonably plentiful there. In the laboratory it was demonstrated that Dolly Varden would feed on terrestrial insects but were slower than cutthroat to switch from benthic to surface feeding, and did so only when bottom food was absent or relatively scarce. When Dolly Varden were near the surface they seemed to locate individual flies as rapidly and from as far away as cutthroat. The cutthroat's habit of hovering and the rapidity with which it became surface-oriented after first capturing a surface prey were obviously advantageous for exploiting surface food. Andrusak and Northcote (1971) found that Dolly Varden in Marion Lake ate considerable numbers of terrestrial insects during June and speculated that this may have been due to a temporary superabundance of surface food. The difference in time required and stimuli necessary to switch from benthic to surface prey apparently may be significant in the segregation process.

Experiments on interactive feeding of cutthroat and Dolly Varden also have revealed differences which may contribute to their segregation in coexistence. When food items were presented at the surface, cutthroat consistently out-scrambled Dolly Varden. Aggression was involved, but spatial position and orientation were also important. Even a small, subordinate cutthroat obtained almost 50% of the surface food ration. When food items were introduced at the bottom and cutthroat were not highly dominant, Dolly Varden got significantly more than cutthroat, probably because of a more vigorous pattern of searching bottom. When food was presented at both levels, Dolly Varden concentrated more on the benthic portion than did cutthroat. This may be due to cutthroat monopolizing the surface, leaving food available to Dolly Varden only at bottom. However, isolated Dolly Varden still captured a preponderance of benthos when prey was available at both levels.

The differences in success between Dolly Varden and cutthroat feeding at low light intensities also may be important to their segregation. If Dolly Varden are indeed capable of feeding in light regimes too low for cutthroat, their potential advantages in sublittoral and profundal regions of the bottom would be increased considerably. Chapman (1966) briefly discussed the importance of visual stimulation to feeding salmonids and noted that bottom organisms must move to be attacked. This generalization may hold true for cutthroat but is less likely to apply to Dolly Varden. In the laboratory it was not the case for either species, but this might have been the result of the fish learning to recognize and expect nonliving foods. Dolly Varden caught more larvae than cutthroat at low intensities, either because they could see better or were less dependent on vision. Both species seemed to rely primarily on vision, as indicated by the sharp increases in larvae captured following a long period of dark adaptation. The Dolly Varden's ability to capture more larvae on bottom at low light intensities may be due to its less discriminatory

feeding behavior. At higher levels of light, it seized and presumably "tested" many objects varying in shape and then rejected or accepted them. Cutthroat, in contrast, seemed to select only specific individual items, which usually were eaten.

If segregation of cutthroat and Dolly Varden in Marion Lake is interactive, then by definition it involves interspecific competition. Andrusak and Northcote (1971) infer that such competition is a significant factor in food segregation of these species. Results of this study indicate that these two species in Marion Lake may have evolved mechanisms for "tolerating" each other so that minimal competitive interaction is now evident between them. Distinct differences in feeding adaptations and spatial preferences are evident, and these are as obvious in solitary individuals as in interacting pairs. It may be unnecessary to infer that food competition now is largely responsible for segregation of the two species. Observed spatial and food segregation could be the result of each species exploiting the habitat it is best adapted for, regardless of the presence of the other. Competition for food at present may not push them apart, although superabundance of food may bring them temporarily together.

The feeding adaptations observed in this study would seem to have evolved as specific benefits toward coexistence of the two species. Possibly, when they first occupied the lake competition between them would have been more intense, but subsequently they may have evolved morphological and behavioral differences favorable to coexistence. Accentuation of differences in sympatry has been described as character displacement (Brown and Wilson 1956) and involves genetic changes in one or more characters (behavioral, physiological, ecological, or morphological). Kohn and Orians (1962), in agreement with this concept, stressed importance of natural selection on ecological characters that, although often less obvious than morphological ones, tend to be more important in determining the degree of coexistence.

Evidence for food competition between fish populations is usually weak or lacking. The period of intense competition probably has ended before most investigations begin, as noted by Johannes and Larkin (1961) in their study of competition for *Gammarus* by sympatric redside shiners (*Richardsonius balteatus*) and rainbow trout (*Salmo gairdneri*). Sympatric populations may often be those that have, through natural selection, evolved ways to coexist with minimal interference.

Is, then, the observed segregation of cutthroat and Dolly Varden in Marion Lake interactive or selective? Interactive segregation between sympatric species may be obvious only in the early stages of their coexistence, as mentioned above. Genetic changes in various morphological and behavioral characters probably develop rapidly where selective pressures are strong. Sheppard (1969) reviews examples from a variety of natural animal populations. It is difficult to decide at what point interactive segregation would become selective segregation if continuous evolutionary differentiation is involved. Certainly it would seem an oversimplification to think in terms of two quite distinct methods of segregation, as suggested by Brian (1956). Both may involve natural selection, the difference being the degree of selection attained. The results of this study indicate that, in Marion Lake, segregation of cutthroat and Dolly Varden may be due to innate morphological and behavioral differences between these species, and that interactive segregation, if occurring there now, is not a dominant factor.

Acknowledgments

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The Bacterial Population in Vertical Flow Tray Hatcheries During Incubation of Salmonid Eggs

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During the incubation period, the number of bacteria on the surface of salmonid eggs in vertical tray hatchery stacks varied between 4.8×10^3 and 10^7 aerobic organisms per square centimeter of egg surface. The bacterial count in the tray water varied between 1.1×10^3 and 5.4×10^5 organisms per milliliter. The most common isolates from the eggs were species of *Cytophaga* and *Pseudomonas*. *Aeromonas hydrophila* was also isolated. These species remained on the eggs throughout incubation, and were also isolated from tray surfaces and tray water.

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Le nombre de bactéries qui peuplent la surface des oeufs de salmonoïdes dans les rayons de plateaux d'incubation à flot vertical varie de 4.8×10^3 à 10^7 organismes aérobies par cm^2 de surface d'oeuf. Le compte bactérien de l'eau des plateaux est de 1.1×10^3 à 5.4×10^5 organismes par ml. Les isolats les plus communs prélevés sur les oeufs sont des espèces de *Cytophaga* et *Pseudomonas*. *Aeromonas hydrophila* a été également isolé. Ces espèces demeurent sur les oeufs pendant toute la durée de l'incubation. Elles ont été aussi isolées de la surface et de l'eau des plateaux.

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THE presence of bacteria on the surface of incubating fish eggs is well established (Oppenheimer 1955; Bell 1966). That this microflora can include bacteria that are pathogenic to fishes is also well documented (McFadden 1969). There is, however, relatively little quantitative information concerning bacteria carried on the egg surface. This is regrettable because such information is important in determining the magnitude of any detrimental effects bacteria may have on the egg surface. Furthermore, the numerous studies which have been made on the metabolism of embryonated eggs (Smith 1957; Blaxter 1969) appear to have ignored this microflora and the contribution it may make to the metabolic parameters measured. This study was initiated, therefore, to gain quantitative information about the microflora. This paper reports the numbers of bacteria present on salmonid eggs during incubation in vertical flow hatcheries, and suggests that greater attention must be given to this microbial flora.

Materials and Methods

EGGS STUDIED

Coho eggs (*Oncorhynchus kisutch*) and chum salmon eggs (*Oncorhynchus keta*) were obtained from the Big Qualicum River project of the Department of Fisheries of Canada in December 1970, and November 1971. Fourteen female coho and three chum salmon were stripped by the incision method. The eggs from each species were fertilized separately, rinsed in river water, and shipped to the laboratory in separate plastic bags of river water contained in ice-packed polystyrene containers. The eggs reached the laboratory 4 hr after fertilization. Rainbow trout (*Salmo gairdneri*) eggs obtained from Lake Penask, B.C., in July 1971 were also examined. The trout were stripped by abdominal pressure, and the eggs were then fertilized, rinsed in lake water, and transported in the same manner as the salmon eggs. One hundred thousand of these eggs were shipped to the Summerland Trout Hatchery of the Department of Recreation and Conservation, B.C., and 10,000 were shipped to the Department of Bacteriology and Biochemistry of the University of Victoria. The stripping, fertilization, and shipping of the eggs was performed by fisheries workers. This allowed for the accumulation of a bacterial load which can be considered representative of the bacterial load normally introduced to other hatcheries receiving eggs.

EGG INCUBATION

When each lot of eggs arrived at Victoria, they were placed in an eight-tray vertical flow hatchery (Heath Techna Corp., Kent, Wash.) that contained 13 liters of water per tray. The eggs of each species were incubated separately in trays containing 3000–5000 eggs. All hatch-

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ery trays were scrubbed and soaked for 2 days prior to use in a povidone-iodine solution (Bridine, British Drug Houses) that contained 1% available iodine. The disinfectant was rinsed from the trays with well water. For the incubation of each lot of eggs, well water (*p*H 7.0 at 11–13 C) was run through the hatchery at 2–3 liters per min. A control eight-tray hatchery operating under identical conditions but containing glass beads was also examined to determine the bacterial population in the absence of eggs. The inclusion of glass beads of the same size and shape as salmonid eggs allowed a comparison between the bacterial numbers on the surface of salmonid eggs with the bacterial numbers on a nonprotein surface incubated in the absence of eggs.

The rainbow trout eggs held at the Summerland Hatchery were held in two four-tray incubator stacks. One incubator stack was supplied with spring water (*p*H 7.3–7.7 at 11.5 C), and the other used a recycled water supply that was made up to volume by the addition of 18.3% (v/v) spring water. The flow rate employed was 18 liters per minute. For bacterial counts on these eggs and their tray water, samples were added to sterile bottles using aseptic techniques. The bottles were packed in ice for transportation and arrived at the laboratory within 12 hr.

Bacteriological Procedures

Using the procedure outlined in "Standard Methods for the Examination of Water and Wastewater" (American Public Health Association 1965), 25 eggs (or beads) were transferred aseptically to a dilution bottle containing 45 ml of buffered distilled water, shaken vigorously 25 times, and duplicate serial dilutions were prepared in buffered distilled water. Samples were also collected from the inlet water, the outlet water, and from each hatchery tray, and duplicate serial dilutions prepared as above. The viable bacteria present were enumerated on standard methods agar (Difco) by the Drop Plate Method (Miles and Misra 1938). Samples were examined for pigment-producing species of *Aeromonas* using furunculosis agar (Difco). Plates were incubated aerobically at 18 C for 72 hr.

Representatives of the most numerous colonial types from all sources were selected from plates containing the highest countable dilution. Coloured photographs of the dilution plates were also prepared to aid organoleptic determination of alterations in microflora. The cultures were then purified and were maintained by weekly transfer on nutrient agar (Difco) and storage at 4 C. Identification of fluorescein-producing pseudomonads was based on the scheme of Stanier et al. (1966). Identification of yellow pigmented organisms was based on the schemes of Hendrie et al. (1966), and Mitchell et al. (1969). Other identification was based on the keys of Skerman (1967) and Breed et al. (1957). Properties of the isolates were also compared with the properties of known stock cultures maintained at the University of Victoria. The media and tests used to partially characterize the isolates were those described by Skerman (1967). Anaerobic conditions required in identification tests were obtained using BBL Anaerobic Jars with Disposable Hydrogen Carbon Dioxide Generator Envelopes (BBL).

Removal of bacteria from the water in the Victoria hatchery was also determined using a washed cell suspension of *Serratia marcescens* (American Type Culture Collection 13880). The growth on 19 hr nutrient agar slant cultures was suspended, washed, and resuspended in sterile well water. A 100 ml aliquot containing 3×10^9 viable cells per milliliter was added to the hatchery inlet. Water leaving the hatchery was sampled at zero time, 1, 4, 48, and 72 hr after addition. The number of S. *marcescens* cells in the effluent water at these times was determined by counting the red-pigmented colonies on the drop plates. Tray surfaces were also swabbed at 24 and 96 hr, and plated on standard methods agar. The plates were incubated at 30 C for 24 hr and then examined for *S. marcescens*. The ability of *S. marcescens* to survive in the water used in the Victoria hatchery was then determined. A washed cell suspension was prepared as above, and the number of viable *Serratia* cells present at zero time and after standing at 12 C for 7 days was determined as above.

Results

The techniques employed to collect and ship the salmonid eggs resulted in bacterial contamination of the eggs. On arrival at the laboratory, the river water containing the salmon eggs carried 1.6×10^4 bacteria per milliliter in 1970, and 2.2×10^4 bacteria per milliliter in 1971. Similarly, the lake water containing the trout eggs had a bacterial count of 1.9×10^4 per milliliter. The bacterial count on the surface of the salmon eggs was between 3500 and 780,000 per square centimeter (Table 1) and the count on the trout eggs was 1.5 million per square centimeter (Table 2). A wide variety of bacterial species were isolated from this water and from the egg surfaces. These were identified as *Achromobacter*, *Alcaligenes*, *Arthrobacter*, *Bacillus*, *Corynebacterium*, *Chromobacterium*, *Pseudomonas*, *Micrococcus*, *Sarcina*, *Vibrio*, and yellow-pigmented species of the *Flavobacterium–Cytophaga* group described by Mitchell et al. (1969). Many of these bacteria were subsequently added to the hatcheries when the eggs were transferred to the incubator trays.

The water supplies also contributed bacteria to the hatcheries. At the Victoria hatchery, the water was passed through a spray nozzle for aeration. This created a visible aerosol, presumably from the venturi action of the spray, and yielded a bacterial load in the inlet water that varied from 100 to 200 organisms per milliliter. Unsprayed well water contained fewer than 100 organisms/100 ml, and the spring water supplying the Summerland incubators contained fewer than 100 bacteria per milliliter, *Pseudomonas fluorescens* and *P. putida*

TABLE 1. Estimated bacterial load on salmon eggs and in the tray water of an eight-tray vertical flow incubator.

Days of incubation	No. bacteria/cm² of egg surface				No. bacteria/ml in tray water			
	Coho eggs in tray 2		Chum eggs in tray 7		Water in tray 2		Water in tray 7	
	1970	1971	1970	1971	1970	1971	1970	1971
0	720,000	16,300	780,000	3500	540	650	360	620
7	7100	61,000	10,500	116,000	9100	16,000	4000	25,600
14	5300	84,000	8700	72,500	8400	68,000	5700	68,800
21	15,600	349,000	28,400	1,260,000	1100	20,000	6300	35,200
28	15,800	59,000	19,200	99,000	1500	50,400	6300	59,200
35	Hatching commenced	570,000	Hatching commenced	670,000	6300	120,000	6800	536,000

TABLE 2. Estimated bacterial load on rainbow trout eggs and in the tray water of vertical flow incubators.

Days of incubation	No. bacteria/cm² surface	No. bacteria/ml of tray water
Eight-tray hatchery at Victoria[a]		
0	1,500,000	150
6	7800	4200
13	110,000	9900
20	10,000,000	11,000
27	8200	2700
Four-tray hatchery at Summerland[b]		
3	4800	7000
7	43,000	1300
14	15,000	2400
21	190,000	2400
Four-tray hatchery at Summerland using recycled H_2O[c]		
3	240,000	1100
7	340,000	1800
14	7300	2600
21	630,000	2500

[a]Tray 3 sampled.
[b]Tray 2 sampled.
[c]Tray 2 sampled; hatchery employed recycled water and 18.3% (*v*/*v*) make-up spring water.

were isolated from the inlet water at both the Victoria and Summerland hatcheries.

Not all of the bacteria entering the hatcheries were able to attach to the available surfaces and so were washed out of the hatchery. This was demonstrated by the addition of 10^{11} viable cells of *S. marcescens* to the inlet water of the Victoria hatchery. One hour after this addition, 4.3×10^6 viable cells of *S. marcescens* were cultured from the outlet water. After 2 hr, 3.4×10^5 per milliliter were detected, and 1.8×10^4 per milliliter were detected after 4 hr. By 24 hr, the count of *Serratia* had fallen to 720 per milliliter, and after 48 and 72 hr, no *Serratia* cells were cultured from the outlet water. Not all of the added *Serratia* cells were washed out of the hatchery. Swabs taken 24 hr after the addition of the organisms revealed that *S. marcescens* was present in low numbers on the hatchery surfaces. The highest concentrations of this tracer organism were found at tray corners, and tray ends, where the water flow had caused the cells to impinge and accumulate. Swabs taken 96 hr after the addition did not yield *S. marcescens*. Although many cells of *Serratia* were washed out of the hatchery, the viability of the organism was not affected by storage in the well water. A suspension containing 3×10^7 *S. marcescens* cells per milliliter yielded 3×10^7 viable cells after storage at 12 C for 7 days.

The bacterial species on the eggs had stabilized after 72 hr incubation. The most common colonial types which appeared on count plates from the salmon and trout eggs had a bright yellow, water-insoluble pigment. The cells from these colonies exhibited typical myxobacterial characteristics and were identified as species of *Cytophaga*. These species remained on the eggs throughout the incubation. Pseudomonads were also isolated from the eggs throughout the incubation. *Pseudomonas fluorescens* and *P. putida* were common isolates, as were *P. fragi* and *P. putrefaciens*. Another common isolate was an *Achromobacter* sp. which was similar to, but not identical with, *A. xerosis*. *Aeromonas hydrophila* was isolated from the trout eggs in both hatchery stacks at Summerland.

Although the bacterial species on the eggs had stabilized after 72 hr incubation, the bacterial num-

bers on the surface of the salmon eggs and in the tray water fluctuated throughout the incubation (Table 1). The bacterial numbers in 1971 were much higher than in 1970. The highest count on embryonated eggs in 1971 was 1,260,000 per square centimeter compared with 28,400 in 1970. Similarly the highest count in the tray water in 1971 was 536,000 per milliliter compared with 9100 per milliliter in 1970. Considerable fluctuation in bacterial numbers on the trout eggs also occurred during incubation (Table 2). The highest count of bacteria on embryonated trout eggs was 10^7 per square centimeter, while the number of bacteria in the tray water varied between 1100 and 11,000 organisms per milliliter.

The bacterial numbers in the control hatchery were much lower. The highest count on the surface of inanimate glass beads was 2100 per square centimeter in 1970 and 2600 per square centimeter in 1971. The number of bacteria in the tray water varied between 310 and 980 per milliliter in 1970 and between 150 and 1100 per milliliter in 1971. The most common isolates were *Pseudomonas fluorescens* and *P. putida*.

Discussion

The number of bacteria accumulated during the collection and shipping of salmonid eggs can be considerable, and may include bacterial species that are pathogenic for fishes. Many of these adventitious bacteria are subsequently added to the hatchery and attach to the hatchery surfaces, while other species can enter the hatchery in the water supply. The bacteria that remain attached to the hatchery surfaces, or to egg surfaces, will then be determined by the temperature, solid content, and the hydrogen ion concentration of the water supply. Not all bacteria are able to attach, or remain attached to the surfaces; this was shown for *S. marcescens*. Although viable in the water supplying one of the hatcheries studied, many of the introduced *Serratia* cells were rapidly washed out of the hatchery. Other bacteria, which are unable to survive in the water supplying the hatchery, are also washed out.

After attachment and subsequent colonization by bacteria, the egg surface and its immediate covering layer can be likened to the "rhizosphere" found in the soil close to leguminous plant roots (Alexander 1961). In this study, species of *Cytophaga* and *Pseudomonas* were able to colonize the eggs. Nutrients are also attracted to the 2000 cm^2 of mechanical surfaces in each tray, and since bacteria grow more efficiently on surfaces (Brock 1966), the vertical tray hatchery behaves as a continuous flow enrichment culture apparatus for bacteria. As the bacteria grow on the surfaces, many of the cells detach and can be detected in the tray water.

Bacteria on the egg occupy only a small portion of the available surface. A coho egg with a surface area of 1.9 cm^2 would be completely covered by a layer containing 2.5×10^8 bacterial cells ($1.5\ \mu m \times 0.5\ \mu m$). The highest count measured on salmon eggs represents a covering of only 1% of this egg surface. Similarly, a trout egg would be covered by a layer containing 1.5×10^8 cells. The highest count of 10^7 bacteria per sq cm represents a covering of only 7.5% of the 1.1 cm^2 egg surface, It must be remembered, however, that because of the problem of removing and culturing all organisms from the eggs, the counts obtained in this study represent a minimum estimate of the total surface microflora.

Although occupying only a small portion of the egg surface, the metabolic activities of the surface microflora might alter the physical and chemical environment of the eggs. Both Oppenheimer (1955) and Bell (1966) have proposed that changes caused by this microflora can result in egg damage. Such damage could occur from the production of toxins and enzymes after the population density of a single species reached 5×10^5 per square centimeter (Brock 1966). The consumption of oxygen by the surface microflora must also be considered. If all the bacteria present on the egg surface were pseudomonads with a dry weight of 10^{-11} g per cell (Brock 1966), and were metabolizing aerobically with a Q_{O_2} ($\mu l O_2$ uptake per mg dry weight per hour) of 150 (Trust unpublished data), then the oxygen demand of the bacterial numbers on the surface of one egg would be up to 15 µliters per hour. In comparison, the oxygen requirements of incubating salmon eggs has been estimated at 0.2 µliter per egg per hour at fertilization, rising to 3.4 µliters per egg per hour at hatching (Blaxter 1969). This bacterial consumption of oxygen could, at times, cause local areas of oxygen shortage in trays containing large numbers of eggs and inadequate water circulation.

It is apparent that bacterial contamination in individual hatcheries will differ depending on the conditions used to collect and incubate the eggs. The number of adventitious bacteria added to hatcheries could be lowered if greater care were taken in the recovery, handling, and shipment of the eggs. However, until such precautions are taken routinely, the transmission of potentially harmful bacterial species will remain a problem. Eggs carrying fish pathogens can contaminate hatchery surfaces, and hatcheries must be adequately decontaminated before subsequent incubations to prevent the transmission of fish pathogenic bacteria to "clean" batches of eggs. Workers interested in eliminating bacterial diseases in their fish populations should

consider collecting the eggs and milt aseptically and incubating the fertilized eggs aseptically. Incubation of such uncontaminated eggs in the presence and absence of selected bacterial species would also aid in determining the effect of bacteria on the development and hatching of eggs. This study has shown that although the bacterial numbers on the egg vary throughout incubation, the numbers are often considerable, and the metabolic processes of these bacteria could well contribute to many of the parameters measured during studies on egg physiology and biochemistry. Workers studying the metabolism of embryonated eggs should also consider the use of axenic eggs to get an accurate measurement of the contributions of the egg to their results.

Acknowledgments

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NOTES

Growth of Larval Herring (*Clupea harengus*) in the Bay of Fundy and Gulf of Maine area[1]

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DAS, N. 1972. Growth of larval herring (*Clupea harengus*) in the Bay of Fundy and Gulf of Maine area. J. Fish. Res. Bd. Canada 29: 573–575.

Initial growth rate for autumn-hatched herring larvae in the Bay of Fundy–Gulf of Maine area is about 2 mm per week. It gradually declines to less than 1 mm per week during the late autumn and winter months, and then increases geometrically in the spring and early summer to an average of 2.5 mm per week.

DAS, N. 1972. Growth of larval herring (*Clupea harengus*) in the Bay of Fundy and Gulf of Maine area. J. Fish. Res. Bd. Canada 29: 573–575.

Les larves de hareng écloses à l'automne dans la région baie de Fundy–golfe du Maine croissent initialement au rythme d'environ 2 mm par semaine. La croissance diminue graduellement à moins de 1 mm par semaine à la fin de l'automne et en hiver, pour ensuite augmenter géométriquement jusqu'à 2.5 mm par semaine en moyenne au printemps et au début de l'été.

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DURING the past 50 years much research effort has been devoted to the study of Atlantic herring, yet our knowledge of the growth and survival of larvae is limited. Of the few significant studies, all except one preliminary report by Tibbo et al. (1958) were made in the northeast Atlantic, mainly in European waters (Bowers 1952; Jensen 1950; Marshall et al. 1937; Masterman 1896). The aim of the present study (see also, Das 1968) was to determine the growth rate of the autumn-hatched larvae in the Bay of Fundy–Gulf of Maine area by following changes in size from month to month.

Materials and methods — Larval herring were collected in St. Marys Bay, the Bay of Fundy, and in the northern region of the Gulf of Maine (Fig. 1) from September 1960 to June 1963. Collections were usually made at monthly intervals with two types of plankton nets: a 1-m (#0 mesh size) nylon net of conventional conical shape, and an Isaacs-Kidd midwater trawl modified to 2-m size. The nets were towed first at 20 m, then raised to 10 m, and finally to the surface. The 1-m net was towed for 5 min at each level at a speed of approximately 2 knots. The Isaacs-Kidd trawl was towed at a speed of 4 knots in the same depth sequence as the 1-m net, but for 10 min at each depth. Larval collections were preserved in 5% formalin.

Before setting tow nets, surface water temperatures were taken at each station.

When large numbers of herring larvae were caught in a tow, a subsample of 100 specimens was examined to estimate the size distribution of the whole sample. Subsamples were obtained either by spreading the larvae evenly over a squared grid and then taking all specimens in squares picked at random, or by taking a grab sample from the total lot stirred in a large beaker of water. When larvae were less abundant, all specimens from the tow were measured. Larvae were measured from the tip of the snout to the distal end of caudal fin, to the nearest half-millimeter.

The autumn spawning in the Bay of Fundy–Gulf of Maine area usually starts in late August, and continues for a period of 8–10 weeks. Herring seem to come in batches to the spawning grounds, and both spawning and hatching occur more or less in "waves." However, there is some overlapping of spawning activity in the area within this period. Because of the length of the spawning season, individual collections usually contain a mixture of individuals at different stages of development; newly hatched and older larvae are often found together. The mean lengths of individual samples, therefore, may not provide a satisfactory method for estimating rate of growth since they are not those of homogeneous groups of larval fish. Length frequencies

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of larvae in pooled samples showed unimodal distribution early in the spawning season but, as the season advanced, the distributions were often bimodal and sometimes multimodal. The general pattern of larval growth could be seen in the shift of histograms to the right, and modal lengths of pooled samples which were easily distinguished in histograms appeared to be the best available means of defining growth curves rather than the mean or median lengths.

Results and discussion — Larval collections for all areas of capture were pooled, and the results plotted as an annual time series (Fig. 2). Collections were usually small between January and March, and the samples did not always show a pronounced mode as in autumn and spring samples. However, the length ranges of those samples were included for uniformity in the treatment of results.

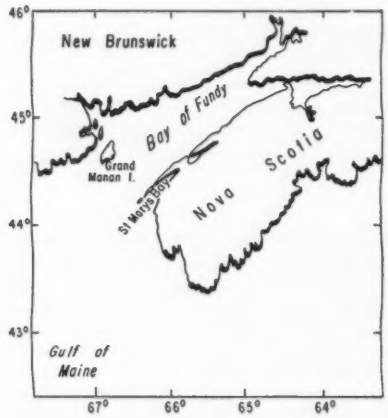

FIG. 1. Map showing the principal localities referred to in this study.

The fall-spawned larvae in the Fundy area usually hatch at a length of 5–9 mm. Most of the specimens caught in September were newly hatched (6–7 mm long) with full yolk sacs. No larvae smaller than 5 mm were captured. During that month surface water temperatures varied between 11.2 and 15.0 C, and larval growth was rapid, averaging 2 mm per week. The modal lengths of the samples collected in the middle of October indicated that the average rate of linear growth of newly hatched larvae was still close to 2 mm per week. The mean surface temperature for October was 11.2 C. From the modes of the samples taken in early November and December it was evident that growth was slower during late October and November, averaging less than 1.5 mm per week. Surface water temperatures were between 6.4–8.7 C in early November of 1960 and 1961, and in 1962 somewhat higher, from 8.2 to 9.0 C. Several other workers have found similar pattern of growth amongst the fall-hatched young in various Atlantic waters (Jensen 1950; Bowers 1952; Tibbo et al. 1958).

The apparent similarities between the size ranges of larvae captured in January and early April (Fig. 2) suggest that perhaps the larval growth was minimal during winter, less than 1 mm per week, or may have stopped. Surface water temperatures varied from 0.9 to 3.8 C in January 1961 and to -0.3–1.3 C at the end of February 1963. The general decline in growth rate in winter also seems to be characteristic of the fall-hatched larvae elsewhere in the Atlantic: Jutland Reef and southern Kattegat, Jensen (1950); Manx waters, Bowers (1952); Scottish waters, Masterman (1896).

The size ranges and modal lengths of the samples taken in April and May indicate that linear growth rate increased in spring, being higher than that of late fall and winter, averaging about 1.5 mm per

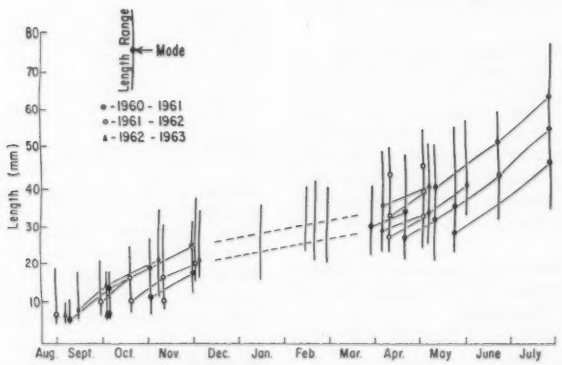

FIG. 2. Model to interpret the growth rates of herring larvae based on the modal lengths of samples.

week in April, and nearly 2 mm per week in May. The mean surface water temperature at the end of March 1961 was 1.7 C, and in early April 1962 and 1963 it was 3.6 and 3.0 C, respectively; it varied from 5.3 C at the end of April to 7.9 C in late May.

Interestingly enough, the present data on growth rate of the fall-hatched larvae during spring in the Fundy area seem to agree with the data on the growth rate of the spring-spawned larvae (over 2 mm per week) from other parts of the Atlantic (Marshall et al. 1937; Jensen 1950; Jean 1956).

Data on the growth rate of larvae in June and July are available for the year 1961 only. However, there is no reason to suppose that the rate of growth in June and July 1961 is not valid for the corresponding periods in 1962 and 1963. Figure 2 indicates that during a period of 9 weeks (May 24–July 27, 1961) growth was close to 22 mm, i.e. about 2.5 mm per week.

In Figure 3 growth curves for herring larvae from the Bay of Fundy–Gulf of Maine area, and from other areas in the Atlantic, for which data are available (Jensen 1950; Bowers 1952; Tibbo et al. 1958), have been plotted together for comparison.

A marked similarity between the growth curves for the early fall-spawned larvae in the Fundy area (A) and Manx waters (a) is evident, but in late autumn, the growth rate in the Fundy area appears to be slightly faster than in Manx waters. However, based on the data available for late autumn and winter in the Fundy area, the differences seem to be of doubtful significance. Tibbo et al. (1958) reported similar instances of faster growth amongst the fall-hatched young in the Bay of Fundy and the Gulf of Maine area. However, their data did not provide adequate information on the rate of growth beyond the month of January, and most of their collections were made on the northern edge of Georges Bank where surface water temperatures during winter were considerably higher than that in the Fundy area. The growth curve (B) for late-hatched fall larvae in the Fundy area shows good agreement with the growth of late-hatched fall larvae in Manx waters (b).

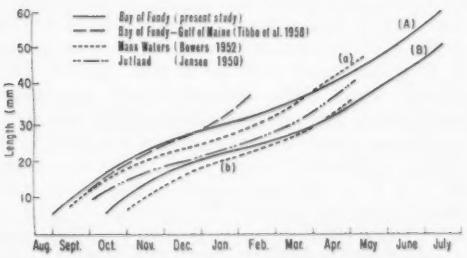

FIG. 3. Comparison of growth rates of autumn-hatched herring larvae from different areas. Aa and Bb represent early and late hatched autumn larvae, respectively.

Figure 3 also shows similarities between the growth curves for fall-hatched larvae in the Fundy area and the Jutland Reef region (Jensen 1950), in that the Jutland curve falls between the two Fundy curves. However, it appears that the growth in Danish waters is somewhat slower during early autumn than that in Fundy region. Jensen (1950), however, did not give any information on sea temperatures in the Jutland Reef region.

The growth curves, for the fall-hatched larvae from the Fundy area and other parts of the Atlantic, thus indicate that growth is rapid during autumn, and in general slows down considerably as winter sets in, as might be expected since conditions of temperature and feeding would be less favourable to growth in winter. It would appear that growth is rapid during autumn spawning while the larvae still bear yolk sacs. Rapid growth in spring is presumably due to the increase in water temperature and to more favorable feeding conditions. Since no detailed temperature data are available with the samples from other areas of the Atlantic referred to in Figure 3, it is impossible at the present time to show any simple relation between temperatures and growth in these areas.

Acknowledgments — I am indebted to Mr S. N. Tibbo for his support and helpful advice during this study, and for his critical review of the manuscript.

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Failure of Bluegill Sunfish, *Lepomis macrochirus*, to Habituate to Handling[1]

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CHISZAR, D., M. MOODY, AND J. T. WINDELL. 1972. Failure of bluegill sunfish, *Lepomis macrochirus*, to habituate to handling. J. Fish. Res. Bd. Canada 29: 576–578.

Two experiments measured changes in breathing rate in bluegill sunfish (*Lepomis macrochirus*) after several forms of routine daily handling. Both experiments revealed large increases in this measure after handling. However, the magnitude of this response did not diminish during 10 days of handling. Thus, the bluegill's respiratory response does not readily habituate to these treatments.

CHISZAR, D., M. MOODY, AND J. T. WINDELL. 1972. Failure of bluegill sunfish, *Lepomis macrochirus*, to habituate to handling. J. Fish. Res. Bd. Canada 29: 576–578.

Nous avons mesuré, au cours de deux essais, les variations du taux respiratoire des crapets à oreilles bleues (*Lepomis macrochirus*) après plusieurs formes de manipulation quotidienne routinière. Les deux essais démontrent une augmentation considérable du taux respiratoire après manipulation. Cependant, l'ampleur de la réponse ne diminue pas en l'espace de 10 jours de manipulation. Nous en concluons que les crapets ne s'habituent pas facilement à ces traitements.

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NUMEROUS investigators have reported handling and related treatments to be stressful to fish. Regurgitation and other digestive complications often result from handling (Windell 1966) and rate of oxygen consumption increases (Black et al. 1939; Ivlev 1938; and others) as does level of lactic acid in the blood (Black 1955). Many of these and other changes may result, at least in part, from increased adrenocortical-steroid output consequent to handling (LeLoup-Hatey 1958; Chavin and Kovacevic 1961).

Similar symptoms follow initial handling in laboratory mammals. However, after routine daily handling, these animals typically habituate (i.e. handling no longer elicits stress responses or the magnitude of the responses are greatly diminished). Indeed, it is common practice to "prehandle" mammals to prepare them for service in certain experiments. The present study asked whether or not fish can be similarly prepared. Prior to employing goldfish in experiments on learning, Mackintosh (1971) routinely handled his subjects during 30-min sessions on each of 5 days. Although this investigator did not measure the extent to which repeated handling resulted in habituation of stress responses, it is implied that these fish performed better in the subsequent experiments than they would have if prehandling had not been administered.

The present study measured the extent of habituation of a respiratory response to handling in bluegill sunfish (*Lepomis macrochirus*). The measure was rate at which the gill covers opened and closed (i.e. breathing rate). Stevens and Randall (1967 a, b) and others have shown this measure to be correlated with oxygen consumption in trout. Shelton (1970, p. 336–337) reviewed respiration data in two species of elasmobranches and six teleost species. Employing these data, we calculated correlation coefficients which revealed that breathing rate (gill-beats per minute) was positively related to ventilation volume (milliliters H_2O/kg per minute; $r = 0.60$, $df = 7$, $P < .05$) and oxygen consumption (milliliters O_2/kg per minute; $r = 0.55$, $df = 9$, $P < .05$). These relations indicate that breathing rate can be used as an indirect index of ventilation, or of oxygen consumption, or both. If breathing rate increases consequent to handling, rate of oxygen consumption probably increases. Also, if the

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magnitude of handling-induced breathing rate perturbation decreases with repeated handling, rate of oxygen consumption probably also decreases (i.e. habituates).

Experiment 1 — Subjects were nine bluegills (approximately 2 years of age) which were seined from a local pond. The fish were maintained for 2 months in a 1000-liter tank containing aerated, carbon-filtered water at 14–17 C and were fed commercial pellets on alternate days during the light portion (7 AM–7 PM) of the day–night cycle. One week prior to the experiment the fish were transferred to individual 30-liter aquaria containing aerated, carbon-filtered water at room temperature (about 19 C). During this acclimation period the fish were never disturbed and were fed daily.

The fish were divided into three experimental groups ($n = 3$). Fish in Group A were gently netted and lifted out of water for 3 sec after which they were gently replaced. Fish in Group B were gently netted but were merely restrained in the submerged net for 3 sec after which they were released. Fish in Group C were gently prodded with a blunt probe for 3 sec. Five minutes before and after each treatment the number of gill beats was recorded. All treatments and measurements were repeated daily for 10 days.

Results — Figure 1 presents the gill-beat rate for the three groups before and after their respective treatments on day 1. Pretreatment baselines were comparable for the three groups ($P > .05$) and all treatments resulted in dramatic increases in this measure ($F = 27.03$, df = 1/6, $P < .01$). Moreover, substantial adjustment ($F = 6.84$, df = 9/54, $P < .01$) occurred by the end of the 5-min post-treatment period. Although Group A appeared to show less post-treatment adjustment than Groups B and C, this difference was not significant ($F < 1$) nor did it appear consistently over the 10 successive days. Thus, the three treatments resulted in approximately equal elevations in gill-beat rate. Since the three groups were statistically equivalent, they were pooled for subsequent analyses.

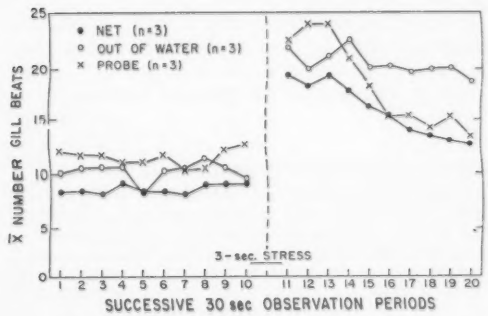

FIG. 1. Mean number of gill beats per successive 30-sec period during pre- and post-stress observation periods for groups A, B, and C.

Habituation could be manifested in two ways in this experiment: (1) the initial post-stress elevation in gill-beats could diminish over days and/or (2) the rate of adjustment during the post-stress period could increase. Either of these phenomena would result in a diminution of gill beats during the post-stress period. To determine if such diminution occurred, the total number of pre-stress gill-beats was subtracted from the total number of post-stress gill-beats for each fish on each day. These difference scores were averaged over the nine fish and the daily means, expressed in beats per second were: .27, .28, .21, .23, .26, .21, .33, .25, .21, and .28. Clearly, there was no tendency for the post-stress increment in gill-beating to decrease over days ($F < 1$).

Experiment 2 — Since experiment 1 showed no evidence of habituation to handling, experiment 2 was performed to replicate one of the previous conditions (Group A) and to extend the analysis to an additional treatment.

Subjects were six bluegill sunfish that were similar in all respects to those employed in experiment 1. Pre-experimental maintenance and acclimation experience were identical to the conditions in experiment 1 except that water temperature averaged slightly greater than 20 C. Three fish (Group A-2) were treated exactly like the fish in Group A. Three additional fish (Group D) were netted on each of 10 days and were placed for 5 min into a second aquarium. This condition was intended to represent the kind of stimulation a fish receives when transferred to an observation tank or to an experimental apparatus. Thus, Group D was expected to reveal the extent to which bluegills habituate to repeated transfer.

Results — The increases in gill-beat rate tended to be somewhat greater than those observed in experiment 1, probably because of higher water temperature. However, Groups A-2 and D did not differ ($F < 1$) indicating that transfer to a second aquarium for 5 min is no more stressful than being netted and held out of water for 3 sec. Finally, there was no evidence that repeated transfer or netting results in habituation as measured by number of gill-beats. Daily averages of the difference scores, expressed as beats per second, were: .51, .53, .49, .51, .42, .51, .56, .50, .54, .50 ($F < 1$).

Discussion — Two experiments failed to produce habituation in the bluegill's respiratory response to a variety of forms of handling. Since laboratory rodents readily habituate to handling, it may be

that such treatments are simply more stressful to fish than to rodents. However, it seems difficult to accept the conclusion that fish do not habituate to handling (especially when handling does not involve removal of the fish from water). Perhaps a more extended series of trials would produce some long-term habituation in the respiratory measure. Or, perhaps other measures of the bluegill's response to handling would reveal acclimation to repeated treatment. However, research in progress in our laboratory has uniformly failed to find habituation in any behavioral response elicited by handling.

Although handling and transportation exert rather dramatic effects on fish, these effects apparently do not interfere markedly with the performance of fish in situations designed to study learning. For example, Mackintosh (1971) transported goldfish (*Carassius auratus*) daily from their aquaria to a water-filled alley in which the fish could obtain food by swimming from a start box to a goal box 32 inches away. Fish were allowed 5 min to recover from transportation at the start of each daily session. (Interestingly, the gill-beat rate of the present bluegills returned almost completely to the pre-stress baseline after 5 min, see Fig. 1). These conditions produced rapid learning in terms of increase in swimming speed to the goal box, indicating that stressful consequences of handling and transportation are not especially troublesome in this situation. In fact, this may explain why fish do not readily habituate to such treatments. Since the stressful effects do not appear to interfere seriously with learning or feeding after a brief recovery period, there may have been little or no selective pressure during evolution to develop mechanisms to subserve habituation. However, an alternative explanation might result from the fact that handling and related forms of stimulation are improbable in the natural situation of fish. In many birds and mammals parental behaviors may generate handling-like consequences in neonates so that evolution may have provided habituation mechanisms. Except for a few species of fish (e.g. chiclids), such parental behaviors do not exist. Thus, there may have been little or no occasion for natural selection to deal with the stressful effects of such treatments in Pisces.

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Karyotypes of the Teleost Family Esocidae[1,2]

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DAVISSON, M. T. 1972. Karyotypes of the teleost family Esocidae. J. Fish. Res. Bd. Canada 29: 579–582.

Representatives of all five surviving species in the teleost family Esocidae, including pikes, pickerels, and muskellunge, and two interspecific hybrids were found to have karyotypes consisting of 50 acrocentric chromosomes. The karyotypic similarity suggests a cytological basis for the ease of hybridization observed among most members of this family and shows that speciation can occur without karyotypic change. Evolutionary implications are discussed.

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Les résultats obtenus démontrent que les cinq représentants actuels de la famille des Esocidae, appartenant au groupe des téléosts ainsi que deux hybrides interspécifiques ont des karyotypes comprenant 50 chromosomes acrocentriques. Cette similarité suggère une base cytologique expliquant la capacité de former des hybrides observée chez la plupart des membres de cette famille et montre que la formation de nouvelles espèces peut se produire en absence de modification de la structure chromosomique. L'évolution de cette famille est discutée.

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THE purpose of this study was to compare karyotypes of all five surviving species of the esocid family, including two subspecies and two interspecific hybrids. Three of these species occur exclusively in North America, one species (northern pike) is found in both North America and Europe, and the fifth species (Amur pike) is limited to Northern Asia. The ease of hybridization among esocid species (Crossman and Buss 1965; Buss and Miller 1967) suggests that the chromosomal complements of these fish do not vary greatly. Prior to the initiation of this study only the European form of northern pike had been karyotyped (Svärdson and Wickbom 1939; Prakken et al. 1955; Lieder 1959; Nygren et al. 1968). While the manuscript was in preparation, karyotypes of the remaining species were published (McGregor 1970; Beamish et al. 1971). This report confirms a diploid number of 50 acrocentrics reported by the majority of these investigators.

Materials and methods—The specimens used were obtained from collections of fish being reared at the Benner Spring Fish Research Station or at other Pennsylvania State fish hatcheries. The four North American species were the northern pike (*Esox lucius*), the muskellunge (*Esox masquinongy*), the chain pickerel (*Esox niger*), and the subspecies redfin pickerel (*Esox americanus americanus*), and grass pickerel (*Esox americanus vermiculatus*). The Amur pike (*Esox reicherti*) were obtained as fertilized eggs from the U.S.S.R. through an exchange program of the U.S. Department of the Interior and reared in Pennsylvania. Two specimens of the hybrid muskellunge × northern pike ("tiger muskie") and one of northern pike × Amur pike were also studied.

The technique used was a modified version of that reported by Ohno et al. (1965). Mature fish were injected intramuscularly just anterior to the dorsal fin with 1–2 cm^2 of 0.5% colchicine 3–4 hr before being killed. The gill filaments from the third and fourth gill arches and tissues from the "head" kidney and spleen were minced into 1-mm pieces and suspended for 30 min in cold, double-distilled water adjusted to *p*H 7 with a sodium citrate solution. Shorter exposure to hypotonic treatment resulted in less cell membrane breakage but gave less well spread metaphase figures. Calcium ions added to the solution in the form of calcium chloride helped to maintain cell membranes but again spreads were not as good. The tissues were then fixed for a minimum of 30 min in fresh 50% glacial acetic acid. Meiotic tissue was obtained from two female muskellunge, two male redfin pickerel, and one female interspecific hybrid between northern pike and Amur pike.

Squash preparations were made from cell suspensions obtained by chopping the fixed tissue pieces in fixative on slides and removing visible tissue pieces before squash-

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ing. The coverslips were removed by freezing the preparations on dry ice; and the slides were air-dried, washed with distilled water, and stained with 1% aqueous crystal violet. Permanent preparations were made using Permount following overnight drying.

Only well-spread, unbroken metaphase cells were used in counting chromosomes. Photographs were made with a Leitz Ortholux Aristophot camera and Kodak 4 × 5 metallographic plates or Ansco Super Hypan 4 × 5 film sheets. Bright light with a green filter and a through-oil system gave the best results.

Results — The chromosomal complements of the five esocid species were remarkably similar. All specimens examined had 50 acrocentric chromosomes with a continuous size range from the largest to the smallest (Fig. 1, 2, Table 1). Karyotypes for *E. niger*, *E. lucius*, *E. masquinongy*, and *E. a. vermiculatus* were identical to those published by Beamish et al. (1971), McGregor (1970), and Nygren et al. (1968) and are not shown.

No species had any visible cytological characteristics which could be used to distinguish it from the others. The hybrids between northern pike and muskellunge, the "tiger muskie", and between northern pike and Amur pike had 50 acrocentrics like the parental species (Fig. 3). No cells with more than 50 chromosomes were observed in any of the specimens, although cells with fewer were

TABLE 1. Chromosome counts and tissues examined in the five species of the family Esocidae and two interspecific hybrids. Note that all unbroken cells had 50 acrocentric chromosomes or 25 bivalents.

Species	Sex	No. of Fish	Tissue	Mitotic cells with $2n = 50$	Meiotic cells with 25 bivalents
Esox masquinongy Muskellunge	Female	4	Gill	17	–
			Kidney	20	–
			Ovary	3	16
Esox lucius Northern pike	Male	1	Kidney	13	–
	Female	3	Gill	16	–
			Kidney	14	–
			Spleen	2	–
E. lucius × *E. masquinongy* "tiger muskie"	Immature[a]	2	Gill	41	–
			Kidney	2	–
Esox reicherti Amur pike	Male	1	Gill	17	–
			Kidney	8	–
	Female	1	Gill	19	–
			Kidney	16	–
			Ovary	1	1
E. lucius × *E. reicherti*	Female	1	Gill	17	–
			Ovary	2	1
Esox niger Chain pickerel	Male	3	Gill	47	–
			Testis	1	–
Esox americanus vermiculatus Grass pickerel	Immature[a]	1	Kidney	1	–
	Male	2	Gill	36	–
	Female	1	Kidney	7	–
Esox americanus americanus Redfin pickerel	Male	2	Gill	26	–
			Kidney	3	–
			Testis	9	10
	Female	2	Gill	25	–
			Kidney	4	–
			Ovary	1	–

[a]Sex in esocids cannot be determined until they reach sexual maturity. Usually "tiger muskie" hybrids are sterile and do not mature sexually.

FIG. 1. Karyotypes of a male (upper) and a female (lower) Amur pike, *Esox reicherti*. Chromosomes are arranged according to size and visibility of secondary arms.

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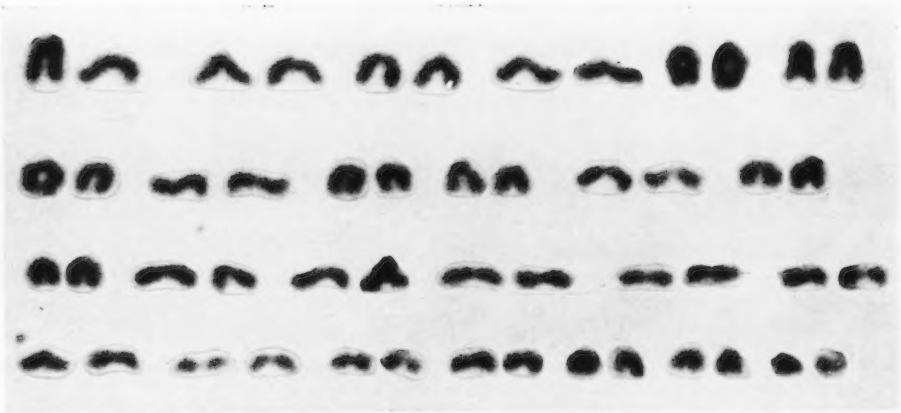

FIG. 2. Karyotype of a female redfin pickerel, *Esox americanus americanus*.

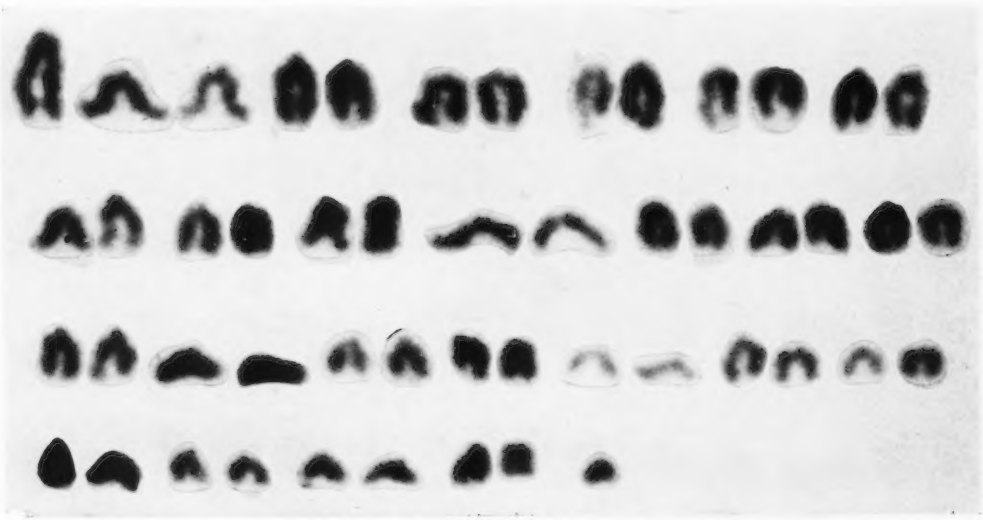

FIG. 3. Karyotype of the hybrid "tiger muskie" between muskellunge and northern pike.

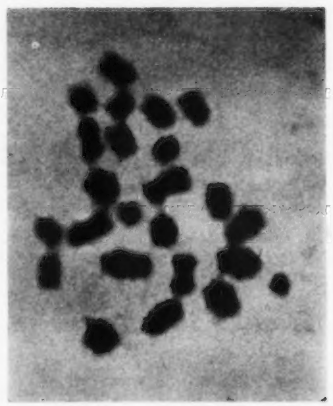

FIG. 4. Metaphase I from a muskellunge female (*Esox masquinongy*) showing 25 bivalents.

seen occasionally. Since these cells were not intact, and usually the chromosome numbers were extremely low, such variation was attributed to cell breakage.

No polymorphism of the Robertsonian type was found either between individuals or within one individual. Centromere-to-centromere associations were seen in a few cells. When the chromosomes were not completely contracted, in late prosphase or early metaphase, an extremely small secondary arm was observed in some. Examples of this are the last chromosome pair in the first row of the Amur male karyotype (Fig. 1) and the first 5 chromosomes in the "tiger muskie" karyotype (Fig. 3).

No heteromorphic sex chromosomes were obvious in either sex of any of the species (e.g. Fig. 1). In the males, cells sometimes had a long chromosome which appeared to have no homologue but this chromosome was not unequivocalby distinguishable in all males and was probably an artifact of differential coiling. An example of this chromosomal difference is shown in the karyotype of the "tiger muskie" (Fig. 3).

In all the gonadal tissues examined, intact pachytene, diakinesis, and metaphase I figures showed 25 bivalents (Fig. 4). A low frequency of what appeared to be polyploid cells (usually $4n$) was observed in the meiotic tissues of both female muskellunge and male pickerel. In gonads which were not undergoing meiosis only a few diploid mitotic cells were ever found. The northern pike $\times$ Amur pike ovary contained a few pachytene cells with 25 bivalents.

Discussion — The finding of identical karyotypes in the five surviving esocid species and two interspecific hybrids is in agreement with previous studies (Nygren et al. 1968; McGregor 1970; Beamish et al. 1971). With three exceptions (Svärdson and Wickbom 1939; Prakken et al. 1955; Lieder 1959) the published data show a stable karyotype throughout the Esocidae. All the North American species from the various locations sampled in this study and those of Beamish et al. (1971) and McGregor (1970) had a constant diploid number of 50 acrocentric chromosomes. One English population (Beamish et al. 1971) and two Swedish populations (Nygren et al. 1968) also had a $2n$ of 50.

The earliest report of $2n = 18$ in pike embryos (Svärdson and Wickbom 1939) is so much lower than all subsequent reports it has been discounted. The photographs of Prakken et al. (1955) and their description of larger chromosomes with "secondary constrictions" and unusual "bends" in the constricted regions indicate that the pike embryos studied by them may have had a diploid number of 50 and that the $2n$ of 48 reported by them resulted from the interpretive problems inherent in the application of the sectioning technique to chromosomal studies. It is also possible, however, that this population differed by a homologous centric fusion from the other pike populations. Lieder (1959), who found a diploid number of 46, suggested that the difference in chromosomal number between the German populations he studied and the Netherlands populations of Prakken et al. (1955) was due to centric fusion, and it may be that some European *E. lucius* populations exhibit intraspecific polymorphism for Robertsonian translocations.

The karyotypic similarity is consistent with the fact that these species hybridize readily (Crossman and Buss 1965; Buss and Miller 1967). Of the 20 possible reciprocal crosses between North American species, 17 produced F_1 progeny and for six the hybrids were fertile (Buss and Miller 1967). Though the ranges of some of the North American species overlap, the species remain separate, suggesting that physical, behavioral, or ecological barriers are involved in maintaining the species. One obvious physical barrier would be the size difference between the muskellunge and the smaller pickerels. The ranges of the two Eurasian forms of pike do not overlap and there is no previous record of artificially produced hybrids; however, successful crosses have been made recently at the Benner Spring Fish Research Station. One may predict that this hybrid will be fertile since 25 bivalents were found in meiosis.

None of the species examined here showed intraindividual chromosomal variation. In the literature reports on chromosomes in this family, such variation was noted only by Nygren et al. (1968) in two *E. lucius* males from Swedish lakes. Kidney cells of these two males had a predominance of $2n = 50$ karyotypes; mitotic cells from testicular tissue showed only $2n = 50$ counts; and 71% of the meiotic cells had 25 bivalents. The remaining cells had fewer than 50 chromosomes. These authors report that morphological comparisons between varying karyotypes were not possible because of overcontraction of the chromosomes. Since their technique was similar to the one used in the present study, in which cell breakage occurred, and since they observed no multivalent formation or aneuploid cells with more than 50 chromosomes, it is possible that chromosomal variation was an artifact of preparation. McGregor (1970) found no variation in chromosome numbers in muskellunge kidney cells, and Beamish et al. (1971) found no variation among gill, spleen, gonad, liver, and fin of the *E. americanus* subspecies.

Nygren et al. (1968) reported polyploid meiotic cells and one triploid kidney cell in the pike they

examined and suggest that the occurrence of nuclei of different sizes in kidney tissue "proves that different cells in this tissue have different chromosomal numbers". Because the kidney in fish contains different kinds of tissue, which may respond differently to hypotonic treatment, it seems more likely that differences in cell size, also seen in the present gludy in gill and kidney, reflect these tissue differences. Although cells of different sizes were found in the five species studied here, polyploid chromosomal complements were not seen in somatic tissues. The finding of multiple ploidies and no multivalent configurations in gonadal tissue in the present study and by Nygren et al. (1968) suggests that the presumptive polyploid cells are really disrupted syncytia of nuclei developing from single germinal cells.

The similarity and stability of esocid karyotypes indicate that chromosomal rearrangement is not a prerequisite to speciation in this group. Artificial crossing eliminates all but gametic and developmental barriers. Since such crosses produce interspecific hybrids in almost all cases and since karyotypes are so similar, the species whose ranges overlap must be maintained by physical and behavioral barriers, such as size incompatibilities and differences in spawning time and place.

Ohno et al. (1969) suggest ancestral fishes had a diploid number of 48 and DNA values 30–40% that of mammals. In view of the DNA values of esocids (32–38%) reported by Beamish et al. (1971) and the stable karyotype of $2n = 50$, the members of this family appear to retain the diploid complement of the ancestral species.

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Effects of Long-Term Exposure to Carbaryl (Sevin) on Survival, Growth, and Reproduction of the Fathead Minnow (*Pimephales promelas*)

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CARLSON, A. R. 1971. Effects of long-term exposure to carbaryl (Sevin) on survival, growth, and reproduction of the fathead minnow (*Pimephales promelas*). J. Fish. Res. Bd. Canada 29: 583–587.

When fathead minnows (*Pimephales promelas*) were exposed to five concentrations (0.008–0.68 mg/liter) of the insecticide carbaryl for 9 months and throughout a life cycle, the highest concentration prevented reproduction and decreased survival. At the high concentration, testes contained motile sperm and ovaries were in a flaccid condition and appeared to be in a resorptive state. At the 0.68 mg/liter concentration, carbaryl appeared to contribute to mortality of larvae (produced by unexposed parents) within 30 days of hatching. Survival of young grown in the 0.008 mg/liter concentration was reduced. Since no demonstrable effects were noted for survival, growth, or reproduction at the 0.017, 0.062, and 0.21 mg/liter concentrations, this low survival value is considered not due to carbaryl. The 96-hr median tolerance concentration (TL 50) and the lethal threshold concentration (LTC) for 2-month-old fathead minnows were 9.0 mg/liter. The maximum acceptable toxicant concentration (MATC) for fathead minnows exposed to carbaryl in water with a hardness of 45.2 mg/liter and a *p*H of 7.5 lies between 0.21 and 0.68 mg/liter. The application factors (MATC/96-hr TL50 and MATC/LTC) both lie between 0.023 and 0.075.

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Lorsqu'on expose des ménés à grosse tête à cinq concentrations différentes (0.008 à 0.68 mg/litre) de l'insecticide carbaryl durant 9 mois et pour la durée d'un cycle biologique, la concentration la plus élevée entrave la reproduction et diminue le taux de survie. A la concentration maximale, le testicule contient des spermatozoïdes doués de mouvement, et l'ovaire est flasque et paraît en voie de résorption. A une teneur de 0.68 mg litre, le carbaryl semble contribuer à la mortalité des larves (issues de parents non exposés) en dedans de 30 jours après l'éclosion. Le taux de survie des jeunes élevés dans une concentration de 0.008 mg/litre baisse. Comme aucun effet appréciable sur la survie, la croissance et la reproduction n'a été observé pour des teneurs de 0.017, 0.062 et 0.21 mg/litre, nous ne croyons pas que le carbaryl soit responsable de cette faible survie. La concentration médiane de tolérance de 96 heures (TL50) et la concentration de seuil léthifère (LTC) des ménés à grosse tête âgés de deux mois ont été établies à 9.0 mg/litre. La concentration toxique maximale acceptable (MATC) des ménés exposés au carbaryl dans de l'eau de dureté de 45.2 mg litre et de *p*H de 7.5 se situe entre 0.21 et 0.68 mg/litre. Les indices d'application (MATC/TL 50-96 h et MATC/LTC) se trouvent tous deux entre 0.023 et 0.075.

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THE objective of this 9 month study was to determine the effects of carbaryl (Sevin[1,2]; 1-naphthyl methylcarbamate), widely used as an insecticide, on growth, survival, and reproduction of the fathead minnow (*Pimephales promelas* Rafinesque) throughout a life cycle.

Numerous carbaryl bioassays of 96 hr or less have been completed with TL50 (median tolerance limit) values determined for a number of fish species (Katz 1961; Stewart et al. 1967; Flores and Fairchild 1968; Macek and McAllister 1970). Information from the above short-term studies

[1]The United States Environmental Protection Agency neither recommends nor endorses any commercial product; trade names are used only for identification.

[2]Product and registered trademark of Union Carbide Corp., New York, N.Y.

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does not provide the knowledge needed on the chronic effects of carbaryl. Recently, several studies (Mount and Stephen 1967, 1969; Mount 1968; Brungs 1969; Eaton 1970; Pickering and Thatcher 1970; McKim and Benoit 1971) have shown significant differences between acute and long-term toxicity values. The concept and methodology used in these continuous flow bioassays and the present study are similar to that described by Mount and Stephan (1967) for establishing safe toxicant limits for fish. They proposed a laboratory measurement of toxicant effects on growth, survival, and reproduction. These measurements of effect are used to determine a maximum acceptable toxicant concentration (MATC) or the no-effect level that lies between the highest toxicant concentration that has no significant adverse effect and the lowest toxicant concentration that has a significant adverse effect. Mount and Stephan (1967) also propose a method for calculating an application factor for estimating the "safe" concentration of toxicants to other species of fish. The factor is obtained by dividing the MATC value by the 96-hr TL50 value. This laboratory-derived factor is then multiplied by the 96-hr TL50 value of other species to be protected to obtain an estimated "safe" toxicant concentration.

Materials and methods — The test chambers were made of stainless steel with one glass end and measured 35 cm wide by 40 cm deep by 45 cm long. Each chamber had a 26-cm standpipe drain and contained approximately 41 liters of test water. The chambers were in a double row and stratified randomly to location.

Growth chambers for young produced were 14 cm wide by 17.5 cm deep by 20 cm long and had 14-cm standpipe drains. Water flows (20 ml/min) were obtained from the main test chambers. Each drain was screened to prevent loss of larvae.

A proportional diluter and injector system for adding microliter quantities of toxicants to water (Mount and Brungs 1967) were used to deliver five concentrations of carbaryl and a control. The diluter flow was divided equally to each of two duplicate test chambers (A and B) at a flow rate of 12 liters/hr. A 50-ml plastic syringe injector contained a stock solution made from 6.746 g of Sevin (80% carbaryl) and 100 ml of acetone. Injection of the toxicant into the water was achieved through a 0.85 mm inside diameter teflon tube attached to a no. 20 Luer end hypodermic needle. The Luer end of the needle was immersed at an approximate 45° angle to the bottom of the diluter toxicant-mixing cell. Thorough mixing was achieved by an airstone under the Luer end.

A double row of cool white fluorescent lights, two lamps of two 40 w tubes, was suspended 200 cm above the water surface. A photoperiod of 10 hr a day was used for the first 3 weeks. This was decreased 1 hr every 3 weeks until a 16-hr photoperiod was reached, which was maintained for 6 weeks. It was then increased 1 hr every 3 weeks until a 14-hr photoperiod was reached. This was maintained for 1 week and then readjusted to a 16-hr photoperiod, where it remained until test termination. This readjustment was made to keep the fish spawning. After a 13-hr photoperiod is reached, fathead minnows revert to a nonbreeding condition. This study was supposed to end when this condition was reached, but the test was continued in order to obtain more data on the effects of the toxicant on reproduction.

Unfiltered Lake Superior water was heated in a headbox apparatus similar to that described by McCormick and Syrett (MS 1970), and a water temperature of 25 ± 2 C was, with several exceptions, maintained in the test chambers. Electrical thermal switches were set to stop incoming test water when the temperature fell to 21 C or rose to 29 C in one test chamber. Water temperature was recorded continuously in one test chamber. Water temperature reached 29 C once during the second month of the experiment and was reduced to 25 C by leaving the tanks in a static condition. On several occasions, water temperature fell to room temperature (18 C); these deviations were not abrupt but took place over several hours.

Acidity, alkalinity, total hardness, *p*H, and dissolved oxygen of the test water (Table 1) were measured according to methods described by the American Public Health Association (1965). Measurements were made on water samples from 10 of the 12 test chambers once each week during the first 7 months of the experiment and on samples from two chambers once each week for the remainder of the test. Test waters were aerated lightly throughout the test.

The carbaryl concentrations in the test chambers (Table 2) were determined by a colormetric method similar to that described by Johnson and Stansbury (1965). Grab samples of water from each test concentration (A or B) and from the control were analyzed at least once a week. Recovery of carbaryl from spiked control water ranged from 91 to 100%.

The exposure was started on April 4, 1970, with a laboratory stock of fathead minnows. Twenty 1–5-day-old larvae were randomly assigned to each test chamber. Their diet consisted of Glencoe Mills[3] trout food fed daily and supplemented weekly with live zooplankton and algae.

Spawning began in early August. Five substrates of cement asbestos, made by halving tiles 10 cm long and 10 cm inside diameter, had been placed in each test chamber. Each half-tile was examined daily for spawn at approximately 10:00 AM, and the daily number of eggs was considered to represent one spawning.

To determine hatchability, 40–50 eggs or embryos, or both, were randomly selected and incubated in egg baskets made of 178-ml bottles with bottoms of fine mesh screen. These baskets were suspended from a shaft that oscillated four times a minute. The contents of the baskets were removed daily, and numbers of dead eggs and/or embryos and larvae were recorded daily. The baskets were cleaned and the live embryos and baskets placed back in the test water. Hatching occurred in 4–6 days.

[3]Product of Glencoe Mills, Glencoe, Minn.

TABLE 1. Mean chemical characteristics (*mg/liter*) of the test water (ranges in parentheses). Measurements were made on water samples from 10 test chambers once each week during the first 7 months of the experiment and on samples from two chambers once each week for the remainder of the test.

Chemical characteristic	Nominal carbaryl concentration (*mg/liter*)					
	0.700	0.233	0.077	0.026	0.009	0.0 (control)
Acidity	1.63 (0.92–3.73)	1.69 (0.92–3.13)	1.47 (0.92–3.14)	1.36 (0.92–2.81)	1.40 (0.92–2.5)	1.32 (0.84–1.88)
Alkalinity	42.4 (40–47)	41.9 (40–45)	42.5 (40–46)	41.8 (40–44)	41.9 (40–44)	42.0 (41–44)
Total hardness	44.9 (41–48)	44.9 (43–47)	45.0 (41–49)	44.9 (41–48)	45.2 (43–48)	45.2 (42–48)
*p*H[a]	7.1 (6.9–7.9)	7.1 (7.0–7.9)	7.2 (7.0–7.9)	7.5 (7.1–7.9)	7.5 (7.0–7.9)	7.6 (7.1–8.1)
Dissolved oxygen	7.1 (5.5–8.1)	7.2 (5.3–8.4)	7.8 (6.8–8.5)	8.0 (7.4–8.8)	8.0 (6.6–8.8)	7.8 (5.7–8.5)

[a]Mode.

TABLE 2. Carbaryl concentrations (*mg/liter*) of long- and short-term test water.

Nominal concentrations (*mg/liter*)	Mean and SD	Range
Long-term tests (42–44 samples)		
0.700	0.681±0.130	0.165–0.990
0.233	0.206±0.059	0.022–0.354
0.077	0.062±0.020	0.008–0.106
0.026	0.017±0.004	0.006–0.029
0.009	0.008±0.003	0.005–0.017
0.0	0.0	0.0
Short-term tests (5 samples)		
16.0	15.66±1.34	13.00–16.60
12.0	10.68±0.65	9.50–11.38
8.0	8.02±0.67	6.90–8.60
6.0	5.88±0.76	4.45–6.60
4.0	4.48±0.27	4.02–4.70
0.0	0.0	0.0

Fifty larvae 1–3 days old were placed in each growth chamber for growth and survival measurements at 30 and 60 days of age. For growth at 30 days, young were removed and photographed by a method similar to that of Martin (1967) and Bushuev (1969). Fifteen of the young were selected randomly and returned to the test chambers.

The same diluter system and an automatic Surg[4] injector were used to obtain a 96-hr TL50 value according to methods described by the American Public Health Association (1965) at a water temperature of 25 ± 2 C. Test waters (A or B) were analyzed daily for carbaryl concentrations (Table 2). Ten 2-month-old fish were used per chamber. A lethal threshold concentration (LTC), as described by Eaton (1970), was also calculated at this time. The LTC was obtained by placing the fish in each of a series of carbaryl solutions. The range of concentrations was selected so that, with a dilution factor of 0.75 between them, greater than 50 but less than 100% mortality would occur in one or more of the higher concentrations and between 10 and 50% would occur at lower exposure levels. The test was continued until the rate of death was 10% or less of the original number of fish in any concentration during the preceeding 24-hr period, the mortality being checked daily. The LTC was considered to be reached at this time.

Reproduction and survival data were calculated at P values of 0.01 and 0.05 with Duncan's new multiple range test for comparing means (Steel and Torrie 1960).

Results and Discussion — Survival of the fathead minnows after 6 months in the 0.68 mg/liter carbaryl concentration (Table 3) was less than in the controls (P = .05). After 9 months at the 0.68 mg/liter concentration, the mean number of eggs produced per female was less than in the controls (P = 0.05), the mean number of eggs per spawning was less than in the four lower concentrations and control (P = 0.01), and no hatching occurred. The mean hatchability percentage of the spawn samples in the 0.68 mg/liter concentration was less (P = 0.01) than those for the three lowest concentrations and the control. At the 0.68 mg/liter concentration, testes contained motile sperm and ovaries were large and robust, contained flaccid eggs, and ap-

[4]Product of Harvard Apparatus Co., Inc., Millis, Mass.

TABLE 3. Survival, growth, and reproduction data for fathead minnows after 9 months exposure, in duplicate tanks, to various concentrations of carbaryl.

	Concentration (*mg/liter*)					
	0.68	0.21	0.062	0.017	0.008	0.0 (Control)
Survival[a] (%)	50;40	65;60	80;70	80;65	65;55	70;75
No. mature males	3;3	5;2	5;4	9;6	9;6	7;6
No. mature females	6;5	8;9	9;6	4;7	4;3	7;6
No. immature fish	0;0	0;2	1;1	1;0	0;1	0;2
Avg total length and weight						
Male (*mm, g*)	54,2.2	59,2.6	57,2.3	64,3.0	55,2.0	58,2.5
	57,2.2	53,2.2	61,2.7	60,2.6	60,2.8	59,2.7
Female (*mm, g*)	51,1.7	52,1.4	49,1.2	51,1.2	50,1.6	50,1.2
	51,1.6	52,1.6	50,1.2	51,1.3	50,1.2	49,1.2
Eggs/mature	20.9	569.1	313.1	545.2	1390	790.3
female	0	876.8	217.3	702.1	751	574.9
Eggs/spawning	19	134	69	121	113	113
(avg)	0	121	87	117	73	138
Hatchability	0(8)[b]	48(27)	59(15)	50(12)	53(17)	64(21)
(%)	–	16(21)	68(8)	66(22)	47(11)	65(13)
Range (%)	0	10–90	0–90	0–88	0–92	34–96
	–	0–70	32–90	18–98	0–90	0–100

[a]Survival of original fish to approximately 6 months of age. Mature males in excess of number of spawning tiles were removed at this time.
[b]Number of samples in parentheses.

TABLE 4. Growth and survival (means and, in parentheses, ranges) of fathead minnow offspring, in duplicate tanks, after 30 and 60 days of exposure to various concentrations of carbaryl.

	Carbaryl concentration (*mg/liter*)					
	0.68	0.21	0.062	0.017	0.008	0.0 (control)
	50 offspring after 30 days					
Survival (%)	30[a];50[a]	88;86	74;58	84;80	46;46	88;96
Length (*mm*)	14.6;11.6	11.8;10.6	11.9;17.1	14.4;11.8	14.0;18.6	12.0;–[b]
	(10–17;7–18)	(6–20;6–19)	(8–20;11–25)	(9–19;8–18)	(9–19;10–20)	(7–21;–)
	15 offspring after 60 days					
Survival (%)	93[a];100[a]	100;93	100;100	100;87	93;100	100;93
Length (*mm*)	22.8;17.7	22.4;21.4	21.6;26.6	21.9;21.6	23.3;24.5	20.0;22.1
	(15–29;10–30)	(18–28;17–34)	(16–34;21–36)	(15–27;15–29)	(14–32;17–38)	(12–36;11–32)

[a]Larvae produced in control.
[b]Data lost as film did not turn out.

peared to be in resorptive condition. Although no statistical tests were used, no differences were apparent in the growth measurements of the original test fish and the offspring between carbaryl concentrations.

The survival of young produced in the controls and transferred to the 0.68 mg/liter concentration at 1–2 days of age and those in the 0.008 mg/liter concentration were less than for the controls ($P = 0.01$) after 30 days (Table 4).

The short-term exposures gave 24-, 48-, 72-, and 96-hr TL50 values, determined by graphical interpolation, of 10.7, 9.2, 9.0, and 9.0 mg/liter carbaryl, respectively, and a lethal threshold concentration of 9.0 mg/liter.

This study demonstrates that a concentration of 0.68 mg/liter carbaryl adversely affects survival and spawning of fathead minnows. At this concentration, carbaryl appears to contribute to mortality of larvae (produced by unexposed parents) within 30 days of hatching, affect the development of eggs and impair egg release, thus preventing the completion of a life cycle. No explanation is advanced for the low survival of young grown in the 0.008 mg/liter concentration. Since this was the lowest concentration tested and no other demonstrable effects were noted for survival, growth, or reproduction at the 0.017, 0.062, and 0.21 mg/liter concentrations, the low survival value is considered not due to carbaryl. Thus the maximum acceptable toxicant concentration (MATC), as defined by Mount and Stephan (1967) lies between 0.21 and 0.68 mg/liter. The application factors for use in estimating the safe level of carbaryl to other species of freshwater fish were calculated using the 96-hr TL50 value of 9 mg/liter and a similar LTC value. The application factors (MATC/96-hr TL50 and MATC/LTC) thus both lie between 0.023 and 0.075.

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Occurrence of Gas-Bubble Disease in Three Species of Bivalve Molluscs[1]

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MALOUF, R., R. KECK, D. MAURER, AND C. EPIFANIO. 1972. Occurrence of gas-bubble disease in three species of bivalve molluscs. J. Fish. Res. Bd. Canada 29: 588–589.

Gas-bubble disease was observed in adult oysters and hard clams held in heated running sea water during the winter. Heating the cold sea water in closed heat exchangers caused it to become supersaturated with atmospheric gases. Exposure of the animals to this water caused the formation of gas-filled conchiolin blisters on the valves of the oysters. Bubbles of gas were observed in the gill filaments of the oysters and clams and in the mantle tissue of the oysters. Any method, such as the use of baffles or an aerated head tank, that reduces the dissolved gas concentration in the water will help prevent the disease.

MALOUF, R., R. KECK, D. MAURER, AND C. EPIFANIO. 1972. Occurrence of gas-bubble disease in three species of bivalve molluscs. J. Fish. Res. Bd. Canada 29: 588–589.

Nous avons remarqué que des huîtres adultes et des quahaugs gardées durant l'hiver dans l'eau de mer chauffée en circulation étaient atteintes de la maladie de la bulle de gaz. Le chauffage de l'eau de mer froide dans des échangeurs en circuit fermé l'a sursaturée de gaz atmosphériques. Au contact de cette eau, il s'est formé sur les valves des huîtres et des quahaugs des boursoufflures de conchioline remplies de gaz. Des bulles de gaz sont apparues dans les filaments branchiaux des huîtres et des quahaugs et dans le tissu du manteau des huîtres. Toute méthode, comme l'emploi de déflecteurs ou l'aération du réservoir de charge, capable de réduire la teneur en gaz de l'eau, contribuera à prévenir cette maladie.

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THIS note describes the occurrence of gas-bubble disease in three species of bivalve mollusc, *Crassostrea virginica*, *C. gigas*, and *Mercenaria mercenaria*. Recognition and prevention of the disease is of particular importance to mariculturists and researchers who maintain these animals in heated flowing sea water during the winter.

Occurrences of gas-bubble disease in fin fish have been well documented in fish hatcheries (Harvey and Smith 1961; Pauley and Nakatani 1967) and in nature (Renfro 1963). A similar disease has been reported in lobsters by Hughes (1968). Marsh and Gorham (1905) reported that molluscs are susceptable to the disease but did not describe their observations or identify the species involved.

We first observed the disease in the clams and oysters during the winter of 1971. In the oysters, the disease first appeared as crescent-shaped conchiolin blisters bordering the mantle. As the disease progressed, conchiolin deposits on both valves became very large causing the mantle and gills to recede. Bubbles of gas were observed in the gill filaments and in the outer layers of the mantle tissue of some individuals. In many animals deposits of mud were observed to collect inside the shell cavity. In severe cases the body of the oyster was reduced to a fraction of its original size as the shell cavity became filled with conchiolin blisters.

Only about 10% of the affected oysters died from the disease, but the survivors continued to be in poor condition until late spring. By June the diseased oysters had covered the conchiolin deposits with shell material, forming hard mud and gas-filled blisters that occupied a significant portion of the shell cavity (Fig. 1 and 2).

Adult hard clams (*M. mercenaria*) held under identical conditions appeared to be less severely affected by the disease than the oysters. Mortalities among the clams were rare. An obvious lightening of the color of the gills was the only gross symptom of the disease in clams. Microscopic examination of the affected gills showed the lack of color to be due to the presence in the gills of numerous trapped gas bubbles that prevented the free circulation of blood.

Analysis of two 10-cm² samples of gas collected by water displacement from conchiolin blisters and gas embolisms in the tissue of 15 diseased oysters showed the gas to consist of 91.2% nitrogen, 6.4% oxygen, 1.2% argon, and 0.5% carbon dioxide. Marsh and Gorham (1905) reported a similar composition of gas

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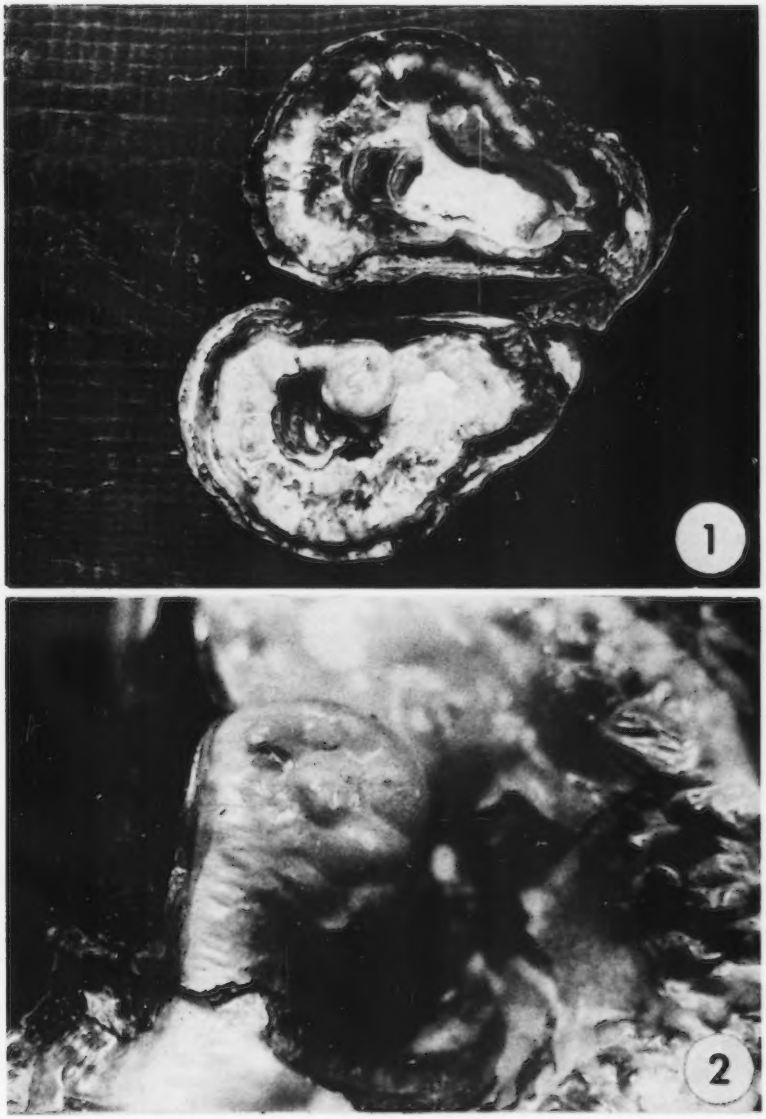

FIG. 1. Valves of an adult oyster, *C. virginica*, showing the effects of gas-bubble disease. The oyster survived the disease and appeared to be recovering.

FIG. 2. Close-up of a large shell blister on the right valve of the diseased oyster. The gas-filled conchiolin blisters had been covered with shell material when these pictures were taken.

taken from fish and lobsters suffering from gas-bubble disease.

As in fin fish (Harvey and Smith 1961; Renfro 1963), histological examination of diseased oysters revealed no pathogenic organism to which the symptoms of the disease could be attributed. The condition results when the animals' external environment is supersaturated with atmospheric gases.

Air forced into solution by suction through leaks in the intake side of a pump can supersaturate the water and cause gas-bubble disease (Marsh and Gorham 1905). Our water systems were carefully checked, but no leaks were found.

During the winter months, occasional failures in our heat exchangers subjected the molluscs to rapid and extreme temperature changes. Failure of the heaters caused the water temperature to drop from 20 C to 2–3 C in a few minutes. When the heaters were again in service, an influx of hot water quickly raised the temperature to 20 C. An experiment was conducted to determine whether this rapid increase in temperature and the resultant reduction in the gas-carrying capacity of the molluscs' body fluids was the cause of gas-bubble disease. Fifty adult oysters, obtained from local waters in February, were divided into five experimental groups and were subjected to the following treatments: 1) immediate initial introduction into 20 C water but without further temperature shock; 2) immediate initial introduction into 20 C water with seven weekly temperature shocks consisting of rapid cooling to 1–6 C, 6 hr of exposure to the cold water, and finally, rapid warming to 20 C; 3) gradual initial introduction into 20 C water with no subsequent temperature shock treatments; 4) gradual initial introduction into 20 C water with temperature shock treatments identical to those in treatment two; 5) maintenance in flowing water at the ambient temperature of 1–6 C with no temperature shock (control). Dissolved oxygen concentrations in the heated and ambient temperature sea water were monitored during the experiment. Oxygen concentrations as high as 129% of saturation were recorded in the 20 C water.

At the end of 8 weeks, examination of the surviving oysters for symptoms of the disease showed no significant relation between the temperature shock treatment and the incidence of disease. Sixty percent of the 20 oysters that were subjected to a weekly temperature shock (groups 2 and 4) showed some symptom of the disease. However, the same symptoms appeared in 75% of the oysters that had been held in water at a constant 20 C (groups 1 and 3). None of the control animals showed any symptoms of the disease.

We concluded that rapid temperature change was not the cause of gas-bubble disease in our brood stock animals. Rather, our observations indicate that the disease was caused by the long-term exposure of the animals to sea water that was supersaturated with atmospheric gases.

It is apparent that gas-bubble disease caused by the use of heated flowing sea water could be a hazard to many mariculture endeavors if preventive measures are not taken. We found that the excess gas could be driven off by allowing the water to cascade over a series of baffles or by strongly aerating it in a head tank before it entered the holding tanks. These precautions prevented occurrence of the disease in clams and oysters that were held in heated sea water during the winter.

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Likelihood Analysis of Three-Way Contingency Tables

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LINDSEY, J. K., AND F. W. NASH. 1972. Likelihood analysis of three-way contingency tables. J. Fish. Res. Bd. Canada 29: 590–591.

The three-way contingency table is considered as an analysis of variance problem. Since the appropriate distribution is multinomial rather than normal, the log likelihood ratios are used to make inferences instead of the variance ratios.

LINDSEY, J. K., AND F. W. NASH. 1972. Likelihood analysis of three-way contingency tables. J. Fish. Res. Bd. Canada 29: 590–591.

Nous considérons les tableaux de contingence à triple entrée pour l'étude des problèmes d'analyse de la variance. Puisque la distribution appropriée est polynomiale plutôt que normale, les inférences sont basées sur les rapports de la vraisemblance plutôt que sur les rapports de la variance.

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CONSIDER a three-way contingency table of size $I \times J \times K$ where individual cells contain counts, $N_{i\,jk}$, of individuals. Suppose the rows one way follow a multinomial distribution. Then, the table may be analyzed as an analysis of variance problem with multinomial "error" and, say, $I \times J$ cells. Then, in the (i, j) th cell, the probability of the k th type of individual occurring will be $p_{i\,jk}$ where $\sum_k p_{i\,jk} = 1$. The maximum likelihood estimates will be

$$\hat{p}_{i\,jk} = N_{ij\,k}/\sum_k N_{i\,jk}$$

and the maximized log likelihood function

$$\log L_{IJ} = \sum_{i'j'k} [N_{i\,jk} \log (N_{i\,jk}/\sum_k N_{i\,jk})].$$

Suppose now that all I rows have the same multinomial distribution, i.e., there is no effect of difference in condition among rows. Then, in the j'th cell of all rows, the probability of the k'th type of individual occurring will be p_{jk} where $\sum_k p_{jk} = 1$ and $p_{jk} = \sum_i N_{i\,jk}/\sum_{i'k} N_{i\,jk}$, so that the maximized log likelihood function is

$$\log L_J = \sum_{i'j'k} [N_{i\,jk} \log (\sum_i N_{i\,jk}/\sum_{i'k} N_{i\,jk})].$$

Similarly, if all J columns have the same distribution, the probabilities will be p_{ik} where $\sum_k p_{ik} = 1$ and $p_{ik} = \sum_j N_{i\,jk}/\sum_{j'k} N_{i\,jk}$ so that the maximized log likelihood function is

$$\log L_I = \sum_{i'j'k} [N_{i\,jk} \log (\sum_j N_{ijk}/\sum_{j'k} N_{i\,jk})].$$

Then, the greater the difference between $\log L_J$ and $\log L_{IJ}$, the more likely is the effect of treatment differences among rows.

If no treatment effect is assumed among either rows or columns, the probabilities will be p_k where $\sum_k p_k = 1$ and $\hat{p}_k = \sum_{i'j} N_{i\,jk}/\sum_{i'j'k} N_{i\,jk}$ so that the maximized log likelihood function is

$$\log L = \sum_{i'j'k} [N_{i\,jk} \log (\sum_{i'j} N_{i\,jk}/\sum_{i'j'k} N_{i\,jk})].$$

A measure of interaction between rows and columns, by analogy with that used in normal theory, is given by $\log L_I + \log L_J - \log L - \log L_{IJ}$. Thus, a table may be constructed, as in normal theory analysis of variance, to analyze the contingency table:

Overall effect	$\log L - \log L_{IJ}$
Between rows	$\log L_J - \log L_{IJ}$
Between columns	$\log L_J - \log L_{IJ}$
Interaction	$\log L_I + \log L_J - \log L - \log L_{IJ}$

Note that the three effects, between rows, between columns, and interaction, are all approximate. For example, the effects between rows and between columns are exact only if there is no interaction

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effect. The exact estimates of these three effects may only be obtained by a very time-consuming iterative process, usually involving problems of overflow with most computers. In numerical examples involving the binomial distribution, little difference was found between the approximate and the exact estimates. If the interaction effect is plausible, log L – log L_I and log L – log L_J are more appropriate for the row and column effects, respectively. But these are also approximate in the same way as the interaction effect: the likelihood equations are nonlinear, requiring iterative solution.

Example 1: An experiment was performed to compare three methods (J) of sampling organisms on the bottom of a stream. Twenty localities (I) were selected at 3-ft intervals along a stream bed. At each location, each method was used in an adjacent area to count the organisms of each of twenty-six species (K) living there. In the analysis, the three sampling methods were compared in pairs:

Methods compared	1 vs 2	2 vs 3	1 vs 3
Overall effect	–5931.76	–4522.65	–3054.20
Between locations	–2183.26	–1852.48	–2596.27
Between methods	–4501.35	–2681.75	–1580.00
Interaction	–752.84	–11.58	–1122.08

We know, from knowledge of the stream, that the distribution of organisms varies with location, i.e., that the effect of location is significant. In making a comparison between effects of location and of method, the numbers of degrees of freedom should be considered: 475 and 25, respectively. Hence, the difference in log likelihood for locations would be expected to be greater than that for methods for the same level of plausibility of effect. These considerations imply that differences between methods 1 and 2 and, to a slightly lesser extent, between 2 and 3 are significant, whereas the difference between 1 and 3, if significant, is much less so.

Example 2: Length–age frequency tables were available for a given species of fish from a number of samples taken in 1 week. We wished to determine if the tables may be combined. At a given age I (=10), the length K (=48) has a multinomial distribution within a given sample J (=6). Then, the analysis is given in the following table:

Overall effect	–301.65
Between ages	–278.83
Between samples	–38.22
Interaction	–15.40

We used the same reasoning as in the previous example. As expected, the length distribution differs among ages, but, since the effect between samples may be considered to be relatively implausible, the samples may be combined with little loss of information about the differences in length distribution at different ages.

As can be seen from the examples, the inferences to be drawn using the likelihood function are "weaker" than those possible when a test of significance is applicable [see, for example, the references provided by Lindsey (1970)]. Differences in maximized log likelihoods are compared to give an indication of the relative size of the various effects, as F-ratios are occasionally compared even although the distribution is known to be non-normal. The comparison using likelihoods will be more accurate than in such cases using the F-ratio, since the additional assumption of normality is not introduced. This remark also applies to considering, for example, –2 (log L – log L_{IJ}) as a χ^2 variate, since the asymptotic normal assumption, being not strictly applicable, has not been introduced.

Of course, the procedure outlined above may be used with any theoretical distribution by replacing the multinomial likelihood function by that for the desired distribution, e.g., the Poisson. When this is done using the normal distribution, the differences in log likelihood corresponding to the various F-tests of analysis of variance result. A simple example, involving inferences using the likelihood function, has been outlined by Lindsey (1970).

An IBM 1130 computer program for the analysis given in this paper is available from the Biological Station, Nanaimo, B.C.

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Identification and Estimation of the Major Components of a Commercial Polychlorinated Biphenyl Mixture, Aroclor 1221

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WILLIS, D. E., AND R. F. ADDISON. 1972. Identification and estimation of the major components of a commercial polychlorinated biphenyl mixture, Aroclor 1221. J. Fish. Res. Bd. Canada 29: 592–595.

The major components of Aroclor® 1221, a polychlorinated biphenyl mixture, have been tentatively identified as the following (weight % composition of each component is given in parentheses): biphenyl (12.7), 2-chlorobiphenyl (28.4), 4-chlorobiphenyl (18.7), 2,2′-dichlorobiphenyl (9.2), 2,4-dichlorobiphenyl (3.5), 2,4′-dichlorobiphenyl (13.6), and 4,4′-dichlorobiphenyl (6.2).

WILLIS, D. E., AND R. F. ADDISON. 1972. Identification and estimation of the major components of a commercial polychlorinated biphenyl mixture, Aroclor 1221. J. Fish. Res. Bd. Canada 29: 592–595.

Les principaux constituants de l'Aroclor® 1221, un mélange biphényle polychloré, ont été identifiés à titre d'essai comme suit (le pourcentage en poids de chaque constituant apparaît entre parenthèses): biphényle (12.7), 2-chlorobiphényle (28.4), 4-chlorobiphényle (18.7), 2,2′-dichlorobiphényle (9.2), 2,4-dichlorobiphényle (3.5), 2,4′-dichlorobiphényle (13.6) et 4,4′-dichlorobiphényle (6.2).

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POLYCHLORINATED biphenyls (PCBs) have been shown to accumulate in marine and other organisms, in both "wild" samples (e.g. Jensen et al. 1969) and through experimental exposure (e.g. Wildish and Zitko 1971). They may affect the activity of enzyme systems in fish (e.g. Yap et al. 1971). They are available commercially as complex mixtures prepared from distillation cuts of the products of the chlorination of biphenyl. Thus far, the composition of commercial preparations has been studied mainly qualitatively (Sissons and Welti 1971; Stalling and Huckens 1971; Tas and DeVos 1971) and in only one case, quantitatively, (Saeki et al. 1970); in that paper, the composition of a PCB mixture containing principally tetra- and pentachlorobiphenyls was described. This note describes the tentative identification and estimation of the major components of Aroclor® (Monsanto Co. Ltd.) 1221, a PCB mixture containing 21% by weight of Cl, by comparisons with synthetic individual chlorobiphenyls. While this work was being carried out, Webb and McCall (MS 1971) reported a qualitative analysis of Aroclor 1221, including all the components listed in Table 1 of this note, and some trichlorobiphenyls not described here.

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Experimental — Biphenyl, monochlorobiphenyls, and 4,4′-dichlorobiphenyl were obtained from Matheson. Coleman, and Bell, and from K and K Labs, Inc. Other chlorobiphenyls were synthesized by the Gomberg–Bachmann reaction, broadly as described by Hutzinger et al. (1971) on a 0.1 mole scale. The crude products were generally obtained as dark oils which were purified by vacuum distillation and/or column chromatography on silicic acid or magnesium oxide. Chromatographic conditions were as follows: silicic acid, Mallinckrodt 100 mesh, activated at 130 C overnight, slurried in *n*-hexane (Fisher Scientific, redistilled) and made up into a column 65 × 3 cm ID; magnesium oxide, "Magnesia 2665 for chromatography" (Fisher Scientific) treated as described by Nicolaides (1970). Samples (2–3 g) were applied to the columns in *n*-hexane, and eluted with this solvent. Yields of pure products ranged from 25–50% of theoretical.

The purity of each product was assessed by thin layer chromatography (TLC), gas–liquid chromatography (GLC), elemental analysis, and (where crystalline products were obtained) melting point (mp) determinations. TLC was carried out on 250 μ layers of silica gel G (Merck) activated 2 hr at 130 C and developed in *n*-hexane; spots were detected by ultraviolet after a silver nitrate spray (Pesticide Analytical Manual 1969). Elemental analyses were carried out on a Perkin-Elmer 240 elemental analyzer. Melting points are uncorrected.

GLC was carried out on a Packard 7400 instrument fitted with a ^{63}Ni electron capture detector (ECD) and

a hydrogen flame ionization detector (FID), or on a Hewlett–Packard 5750 instrument fitted with a ^{63}Ni ECD. Conditions were as follows: columns, 6 × ⅛ inch ID glass, packed with (a) 3% DC-200 on 100–120 mesh Gas Chrom Q operated at various temperatures between 140–165 C; (b) 2% DEGS on 100–120 mesh Chromosorb G operated at 170 C; and (c) 3% Dexsil 300 on 100–120 mesh Gas Chrom Q operated at 240 C. Injection port, 170 C (260 C for Dexsil); detector, 180 C (280 C for Dexsil); carrier gas, N_2 at 40 ml/min, or, (in the Hewlett–Packard instrument), 10% methane in argon at 40 ml/min.

Injections were made with Hamilton No. 701N syringes, and peaks were recorded on Honeywell recorders fitted with Disc Instrument, Inc., integrators. Kovats retention indices (Sissons and Welti 1971) were determined by coinjection of chlorobiphenyls with *n*-alkanes (C_{14}–C_{20}) using a FID system.

Structures were assigned to the major components of Aroclor 1221 by comparison of retention times of the Aroclor peaks with those of synthetic chlorobiphenyls on both polar and nonpolar columns. Estimates of Aroclor peaks were made from calibration curves prepared for the ECD response for the appropriate chlorobiphenyl in the 1–40 ng range on the DC-200 column only. Biphenyl was chromatographed on a DC-200 column, detected by FID, and estimated in Aroclor 1221 from a calibration curve prepared in the 20–200 ng range.

Results and discussion — All chlorobiphenyls studied ran as single spots on TLC or as single peaks on at least two columns on GLC. Melting points of crystalline compounds generally agreed with those reported in the literature. 2,4-, 2,6-, and 3,4-dichlorobiphenyl could not be crystallized; all these compounds are reported to have low mps, however, in one case (2,4-dichlorobiphenyl: 24–25 C) around room temperature. Data for 2,4′-dichlorobiphenyl and for the compound tentatively identified as 2,4,2′-trichlorobiphenyl (mp 83–85 C) have not been reported in the literature.

Table 1 lists the major components and the levels at which they occur in Aroclor 1221. Biphenyl, and mono- and dichlorobiphenyls constituted the bulk of the mixture. Only 2- and 4-substituted compounds were observed; this is in agreement with the view (based on resonance considerations, Gould 1959) that chlorination of biphenyl would take place preferentially at the 2- and 4- positions. However, 3- and 5- substituted chlorobiphenyls are observed in more highly chlorinated mixtures (e.g. Sissons and Welti 1971; Tas and DeVos 1971).

Figure 1 identifies the major components of Aroclor 1221. The ECD response curve shows no peak for biphenyl, but its point of emergence (established from a FID response curve) is indicated. The unidentified peaks following 4,4′-dichlorobiphenyl probably represent trichloro compounds, though none corresponded exactly to synthetic 2,4,6-trichlorobiphenyl or to the products of our attempts to prepare 2,4,2′- or 2,4,4′-trichlorobiphenyl. The latter two products were not identified with any certainty, however. (Sissons and Welti (1971) have identified 2,4,2′-, 2,4,4′-, and 2,6,2,′-trichlorobiphenyl in

TABLE 1. The major components of Aroclor 1221.

Compound	wt (%) in Aroclor 1221
Biphenyl	12.7
2-chlorobiphenyl	28.4
4-chlorobiphenyl	18.7
2,2′-dichlorobiphenyl	9.2
2,4-dichlorobiphenyl	3.5
2,4′-dichlorobiphenyl	13.6
4,4′-dichlorobiphenyl	6.2
Total wt (%) Aroclor 1221 accounted for	92.3
Calculated wt (%) Cl of above composition	19.6

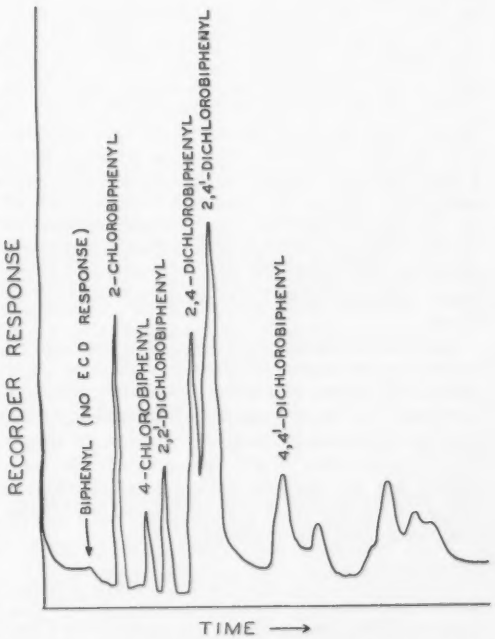

FIG. 1. ECD Response curve of Aroclor 1221, on DC-200 at 155 C (conditions as described in text) identifying major components.

Aroclor 1254, and it seems probable that these would occur in Aroclor 1221 to some extent.) The apparent abundance of these peaks is attributable to their intense ECD response; on a weight-for-weight basis, trichlorobiphenyls may have up to 20 times the ECD response of dichlorobiphenyls (Zitko et al. 1971).

The composition quoted in Table 1 accounts for 92.3% (by weight) of Aroclor 1221; total Cl content calculated for such a composition is 19.6% by weight. The discrepancy of 7.7% in weight composition may be attributed partly to experimental error in estimations, and partly to the fact that some compounds present in Aroclor 1221 have not been identified or accounted for.

Since 2,4′-dichlorobiphenyl (one of the components of Aroclor 1221) is a compound hitherto unreported in the literature, we describe here the results on which we base this structure.[1] 2,4′-dichlorobiphenyl was prepared by the Gomberg–Bachmann reaction using 4-chloroaniline and chlorobenzene; this reaction is not unambiguous, however, as 3,4′- and 4,4′-dichlorobiphenyl may also be synthesized. The 4,4′- compound can be readily identified among the reaction products from its mp and GLC retention behavior; these data are already available in the literature (Hutzinger et al. 1971). The assignment of the 2,4′- and 3,4′- structures to the other products was made from predicted Kovats retention indices calculated by the method of Sissons and Welti (1971). Results of these calculations are shown in Table 2. It is clear that agreement between predicted and observed retention indices for compounds of known structure is close, and that there is sufficient difference between the predicted retention indices of 3,4′-dichlorobiphenyl and 2,4′-dichlorobiphenyl to allow the identification of both these compounds. Observed and predicted retention indices for the other major Aroclor 1221 peaks are included in Table 2.

Carbon and hydrogen analyses performed on the presumed 2,4′-dichlorobiphenyl agreed closely with theoretical values, and a mass spectrum run on it confirmed its identity as a dichlorobiphenyl, but gave no information about the position of substituents. A 60-MHz NMR spectrum of this compound did not provide sufficient information to define the position of the substituted Cl atoms. The compound had a mp of 41 C.

[1]Note added in proof: A 220 MHz NMR spectrum run on our presumed 2,4′-dichlorobiphenyl was consistent with this structure, and inconsistent with a 3,4′- substitution pattern. Our 2,4′-dichlorophenyl was similar in chomatographic behavior and melting point to a sample prepared by an unambigious route by O. Hutzinger (personal communication).

TABLE 2. Calculation of predicted Kovats retention indices for some chlorobiphenyls on DC-200 at 140 C (conditions as described in text).

Compound	RI (observed)	½ RI	Predicted RI (sum of two ½ RIs)
Biphenyl	1358	679	–
2,2′-diCl	1572	786	–
4,4′-diCl	1721	860.5	–
2-Cl	1467	–	1465
4-Cl	1538	–	1539.5
3-Cl[a]	1531	–	–
2,4′-diCl	1644	–	1646.5
3,4′-diCl[a]	1714	–	1712.5
2,4-diCl	1622	–	–

[a]Not observed in Aroclor 1221.

It should finally be noted that, in our experience, the composition of more highly chlorinated PCB mixtures (Aroclors 1254 and 1260) varies slightly depending on the source of these materials. This probably reflects some variation from batch to batch during production. The analysis shown in Table 1, therefore, describes only that sample of Aroclor 1221 available to us and should be taken only as a guide to Aroclor 1221 composition.

Acknowledgments — Aroclor 1221 was a gift of Monsanto, (Canada) Ltd. Mass and NMR spectra of 2,4′-dichlorobiphenyl were determined by Drs S. H. Safe and S. Ray.

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Winter Geostrophic Circulation in the Gulf of St. Lawrence

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EL-SABH, M. I., AND O. M. JOHANNESSEN. 1972. Winter geostrophic circulation in the Gulf of St. Lawrence. J. Fish. Res. Bd. Canada 29: 595–598.

The field of winter geostrophic circulation at the surface of the Gulf of St. Lawrence has been calculated for the first time. The dynamic method has been applied with Defant's method used for determining a variable reference layer. The main features of the reference layer are the three depressions, west and southeast of Anticosti Island and at the middle of Cabot Strait. The existence of two gyres (anticlockwise west and clockwise southeast of Anticosti Island), the outflow on both sides of Cabot Strait, and inflow at the middle of it are the dominant features in the winter surface circulation. A net volume transport through Cabot Strait in February 1962 was found after adjustment for zero salt transport, to be 6×10^3 m^3/sec in the outward direction.

EL-SABH, M. I., AND O. M. JOHANNESSEN. 1972. Winter geostrophic circulation in the Gulf of St. Lawrence. J. Fish. Res. Bd. Canada 29: 595–598.

Les auteurs ont calculé pour la première fois le champ de circulation géostrophique hivernal à la surface du golfe Saint-Laurent. Ils ont utilisé la méthode dynamique, jointe à celle de Defant pour la détermination d'une couche de référence variable. Les principales caractéristiques de la couche de référence sont les trois dépressions situées à l'ouest et au sud-est de l'île d'Anticosti et au milieu du détroit de Cabot. L'existence de deux tourbillons, l'un en sens inverse des aiguilles d'une montre à l'ouest et l'autre, dans le sens des aiguilles d'une montre au sud-est de l'île d'Anticosti, la sortie de l'eau de chaque côté et l'entrée au milieu du détroit de Cabot sont les caractéristiques dominantes de la circulation superficielle en hiver. Le volume net du transport d'eau par le détroit de Cabot en février 1962 a été calculé, après correction pour un transport de sel de zéro, à 6×10^3 m^3/sec en direction de l'extérieur.

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A description of the circulation in the Gulf of St. Lawrence has been based largely on scanty current observations and the application of the geostrophic methods. Most of these circulation studies in the Gulf have been carried out during the ice-free months, consequently little is known about the winter circulation when ice in varying concentration is present. This note is the first attempt to study the geostrophic circulation during winter.

The Gulf of St. Lawrence has an area of 214×10^3 km^2 (Forrester and Vandall MS 1968) with two main openings to the Atlantic Ocean: Cabot Strait and Belle Isle Strait. The Laurentian Chan-

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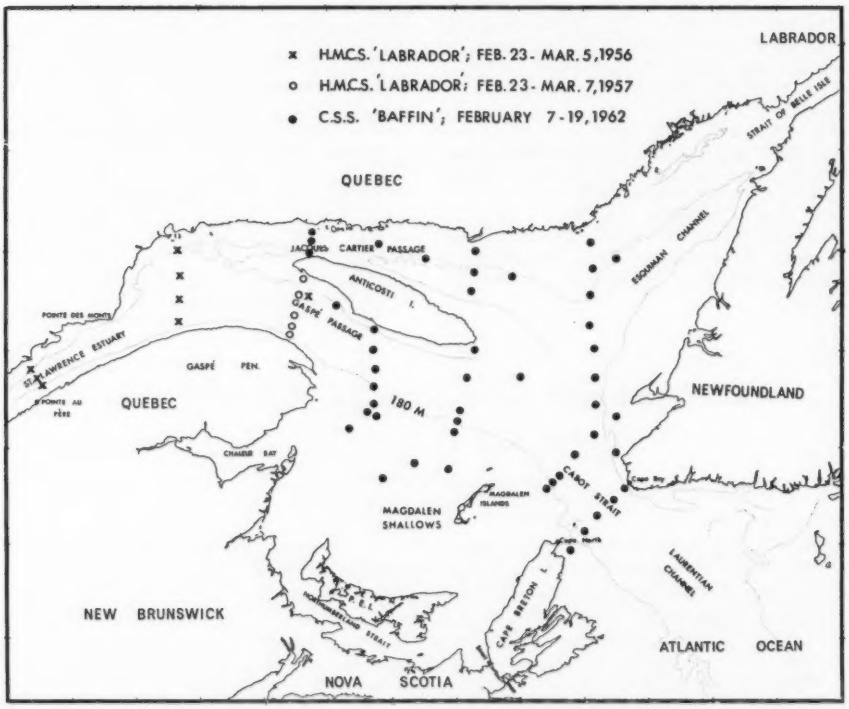

FIG. 1. Location of winter stations employed.

nel and Magdalen Shallows are the main features of the Gulf's bathymetry (Fig. 1). The former is a deep trench stretching from the Atlantic Ocean to the lower St. Lawrence River, ranging in depth from 600 to 250 m, while the typical depths of the latter are less than 50 m. One quarter of the Gulf area is shallower than 50 m, whereas a fifth is deeper than 300 m (Lauzier et al. 1957).

Materials and methods — For the purpose of this investigation, an attempt was made to choose data that would represent the normal conditions during winter in the Gulf. Figure 1 shows the location of the winter stations employed.

The Gulf has a complex topography with large shallow portions. It was felt, therefore, that a variable reference level for converting the relative velocities into absolute velocities would be more realistic than a constant reference depth. Following a technique described in Neumann and Pierson (1967), the variable reference layer was calculated using Defant's method (Defant 1941). Specific volume anomalies (SVA) at the originally observed depths for each oceanographic station were read from the Canadian Oceanographic Data Centre reports. SVA values were then interpolated for every 5 decibars, applying the interpolation scheme described by Reiniger and Ross (1968), before the dynamic calculations were performed. Interpolation of SVA, dynamical calculation, geostrophic current, and volume transport through Cabot Strait were carried out on an IBM 360 computer.

Results and discussion — Figure 2 shows the depth of the reference layer. It is characterized by a steep slope along the central part of the Gulf, three depressions in the Laurentian Channel, southeast and west of Anticosti Island and in the central region of Cabot Strait, and rising toward the North Shore. It varies from 30 to 40 m in the Magdalen Shallows to more than 300 m in part of the Laurentian Channel. Reference to bathymetric charts indicates that the topography of the zero reference layer in general follows the same shape as the bottom topography. Figure 3 shows the absolute topography of the sea surface.

In the western part of the Gulf, the Gaspé current, the anticlockwise gyre, and the inflow along Anticosti Island are the dominant features, as they are during the ice-free months of the year (El-Sabh et al. MS 1969). Farquharson (MS 1966) has shown that the Gaspé current on occasion might even disappear during the summer, but our rather

scanty data give no possibility of looking into the variability of the circulation.

A fairly consistent picture observed during the summer months, southeast of Anticosti Island, is the existence of a large anticlockwise gyre as evidenced by drift bottle experiments (work by Lauzier, Lawrence MS 1968) and by theoretical models (Blackford 1966; Murty and Taylor MS 1969). From Fig. 3 it is obvious that no such gyre is evident in winter. On the contrary, a smaller clockwise gyre has been observed southeast of Anticosti Island. In general the gyres are associated with depressions in the zero reference layer.

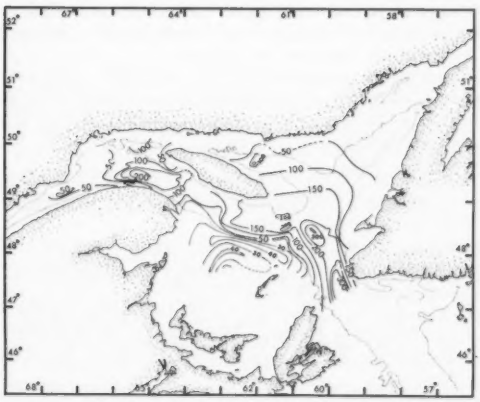

FIG. 2. Depth (*m*) of the reference layer for winter dynamic computations in the Gulf of St. Lawrence.

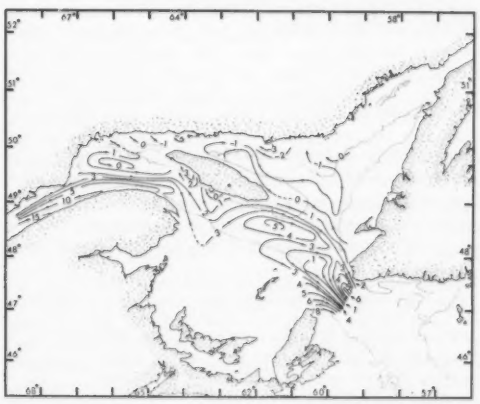

FIG. 3. Winter sea surface topography in the Gulf of St. Lawrence. Figures indicate the deviation of the sea surface from a level surface in dynamic centimeters based on the variable reference layer shown in Fig. 2.

The surface flow through Cabot Strait is outward on both sides, stronger on the Cape Breton side, which agrees well with the drift bottle experiments at that time of the year (Bumpus and Lauzier 1965). An interesting feature is the strong inflow of surface water through the middle of the strait which is diverted to the north and south and joins the outflowing current on both sides of it. This "blocking" of inflowing surface Atlantic water might be due to the prevailing NW wind regime over the Gulf during the winter months, and also to the influence of drifting ice. The geostrophic current and volume transport have been calculated for a vertical section through Cabot Strait, using the Baffin (1962) February cruises, based on the reference layer described earlier. Figure 4 shows the vertical distribution of the geostrophic velocity field through the strait. On the Cape Breton side the outflow is strongest in the upper layer reaching a speed of 26 cm/sec. This flow decreases with depth and reverses its direction below 300 m between stations 9–10. Between stations 10–11 strong inflow down to 250 m occurs with the velocity in the upper layer reaching 35 cm/sec. Along the Newfoundland side of the strait outflow down to 200 m takes place, with no significant motion below this depth. The volume transport through the strait was calculated and an adjustment was made to satisfy the assumption of zero salt transport through the section. The adjusted volume transport was

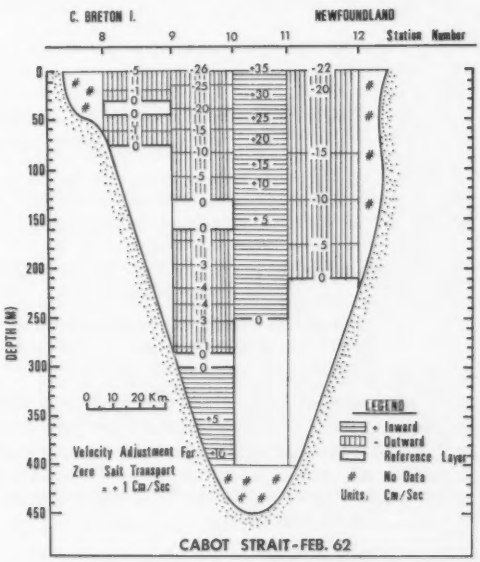

FIG. 4. Geotrophic velocity for Cabot Strait, February 1962.

6×10^3 m^3/sec outwards, which agrees well with the average net volume transport from river discharge and run off (Trites MS 1970).

We would stress that this is a first approximate picture of the geostrophic winter circulation and our data do not allow us to draw any conclusion about the variability of the circulation. This study might be useful, however, for planning further experiments in the investigation of the winter circulation in the Gulf and it might also be used as a rough estimate of geostrophic surface flow in ice studies and prediction problems.

Acknowledgments — We wish to thank Drs E. M. Hassan and W. D. Forrester of the Bedford Institute for their valuable comments and criticism of the manuscript.

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Some Effects of Group Housing Upon the Aggressive Behavior of the Lobster *Homarus americanus*

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DUNHAM, P. J. 1972. Some effects of group housing upon the aggressive behavior of the lobster *Homarus americanus*. J. Fish. Res. Bd. Canada 29: 598–601.

Lobsters maintained in a group housing tank for 36 days were less aggressive than lobsters maintained in individual tanks. A measure of activity indicated that differences in aggressive behavior could not be explained in terms of activity differences between the two groups.

DUNHAM, P. J. 1972. Some effects of group housing upon the aggressive behavior of the lobster *Homarus americanus*. J. Fish. Res. Bd. Canada 29: 598–601.

Des homards gardés dans un vivier à abri commun durant 36 jours sont moins agressifs que ceux maintenus en viviers individuels. Une mesure de l'activité démontre que ces différences dans le comportement agressif ne peuvent s'expliquer en termes d'activité différentielle des deux groupes.

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THE lobster *Homarus americanus* has traditionally been described as a very solitary, aggressive animal (Herrick 1911; Knight 1918); these descriptions have been substantiated in more recent underwater observations of the animal in its natural environment (Cobb 1971; Thomas 1968). These descriptions of the lobster's behavior in the field are, however, somewhat inconsistent with observations in high population density holding tanks. For example, Cobb (1971) provided lobsters with limited shelter in a communal tank and found that they would share the available shelter. Some personal observations of lobsters in communal tanks indicate that both aggressive and nonaggressive social interactions occur; i.e., some animals group together in one corner of the tank while others exhibit more aggressive, territorial behavior.

These observations of behavior in a group tank suggest that exposure to the high population density of the group tank might inhibit aggressive behavior. The purpose of the present experiment was to determine if exposure to group housing attenuates the aggressive behavior of the lobster.

Methods and materials — Sixteen male lobsters with a carapace length of 115 ± 3 mm were purchased from Burn's Fisheries, Halifax, N.S. The chelae had been immobilized with wooden pegs that were removed when the animals were placed in holding tanks for 2 weeks of adaptation to laboratory conditions. All animals were coded with small holes punched in the uropods and all appeared to be in the hard shell stage C of the intermolt cycle (Passano 1960).

Laboratory conditions — All tanks in the laboratory were constructed of marine plywood with a light gray epoxy paint finish. A plate glass front facilitated observation of the animals. The tanks were supplied with unfiltered, nonrecirculating sea water at the approximate rate of 8 liters/min. During the course of the experiment the water temperature varied between 15 and 17 C. A 12-hr day–night cycle was maintained by automatic timers with lights coming on at 0900 hr each day. The standard feeding procedure consisted of providing fresh cod every 2 days and maintaining a continuous supply of live clams on the bottom of the tanks. Uneaten cod was removed at each feeding interval.

Treatment procedure — After the initial 2-week holding period, the lobsters were randomly assigned to two groups of eight animals. The animals in group IH were housed in individual tanks 16 cm wide, 30 cm long, and 30 cm deep that were constructed by placing plywood dividers in a long narrow tank. The dividers were perforated with small holes to permit water to flow from a central unoccupied compartment through the occupied tanks, and into two end compartments which contained standpipe drains. Animals in Group CH were housed together in a large communal tank that was 100 cm wide, 80 cm long, and 55 cm deep.

The differential housing treatment continued for 36 consecutive days before test procedures were started.

Test procedure — Tests of aggressive behavior were conducted in a separate tank which contained a live male lobster of 133-mm carapace length as a target. The test tank was 100 cm wide, 80 cm long, and 55 cm deep. A small cave was formed in one corner of the test tank by placing a rock next to the standpipe. The cave was approximately 8 cm deep and provided only partial shelter for the target animal.

Certain conditions were standard during all tests. Two animals from each group were tested each day. All testing was conducted between 1900 and 2100 hr and the treatment conditions were counterbalanced to control for any effects of the order of testing. Water flow to the test tank was stopped 1 hr before each test and all food and detritus was siphoned from the tank. A single 100-w incandescent bulb was suspended from the center of the test tank at a height of 90 cm above the water surface.

Under these conditions, the test phase of the procedure was divided into two types of test. First, a preliminary test was conducted on days 37–40 of the experiment to determine if the differential housing treatment had any effect upon the activity of the animals or their tendency to seek shelter. In this test each experimental lobster was placed in the test tank, without the target lobster, and the amount of time spent exploring the tank prior to occupying the available shelter was recorded. In each instance, it was observed that the lobster explored the tank continuously until the shelter was occupied, at which time activity ceased for the remainder of the observation period.

On days 41–44, the target lobster was returned to the shelter in the test tank and each of the experimental lobsters was introduced for a half-hour observation period during which the frequency and duration of the aggressive attacks directed at the target animal were recorded over the three successive 10-min periods. The onset of an aggressive attack was defined as that point when physical contact was made between the two animals. Similarly, the termination of physical contact was considered to be the termination of an aggressive interaction. Although this operational definition of aggression does not include some of the early behavioral components in an aggressive interaction (e.g. meral spread), it has the advantage of being a more objective measure.

Results of activity test — A measure of the amount of time spent exploring the chamber prior to occupying the available shelter revealed no significant differences ($t = .03$) between group IH (923 sec) Group CH (936.3 sec). Hence, the differential housing treatment did not alter the lobsters' activity and/or tendency to seek shelter.

Results of aggression test — Figure 1A illustrates the average frequency and duration of attacks on

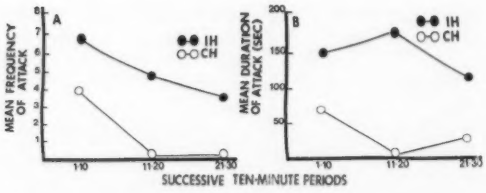

FIG. 1. Average frequency (A) and duration (B) of attacks during successive 10-min periods.

the target animal by lobsters in Group CH and IH during successive 10-min periods of the half-hour aggression test. Animals maintained in individual tanks were clearly more aggressive than animals housed in communal tanks.

Analyses of variance indicated that the differences were significant between the two groups on both the frequency ($F = 19.74$, $p < .01$) and duration ($F = 5.60$, $p < .05$) measures. There was also a significant decline in frequency of attacks over the successive 10-min periods ($F = 15.41$, $p < .01$).

Discussion — The results of the experiment support the observation that lobsters housed in communal tanks are less aggressive than those housed in solitary conditions. The preliminary test revealed no differences in activity between the groups, hence it is difficult to argue that the difference in aggression is indirectly caused by differences in activity or exploratory behavior.

Also, there were qualitative differences in the aggressive behavior exhibited by the two groups of lobsters. For example, lobsters from Group IH typically approached the target lobster with a direct frontal attack preceded by meral spread and antenna fencing. This type of aggressive encounter is similar to other descriptions of aggressive behavior observed between isolated lobsters (Scrivener MS 1971; Atema and Engstrom 1971), and can be contrasted with the behavior of the lobsters in Group CH. Several of the latter, for example, were observed to approach the target lobster tail-first without evidence of the preliminary display behaviors such as meral spread and antenna fencing.

The differences obtained in the present experiment are congruent with observations of the aggressive behavior of other decapod crustaceans. Hazlett (1968) observed the aggressive interactions between pagurid hermit crabs (*Pagurus bernhardus*) in high population density containers. The frequency and intensity of aggressive behavior observed in a group of crabs declined over a period of 60-min exposure to the group situation. This decline is similar to the decline in the frequency of attacks observed in the present experiment. Both observations suggest that exposure to conspecifics attenuates the aggressive behavior of the animal.

Hazlett (1966) also examined the effects of social isolation upon the aggressive behavior of the shallow water hermit crab *Calcinus tibicen* found along the shores of some Caribbean islands. Isolation increased the frequency of aggressive encounters measured subsequently in a group test tank.

These experiments with crabs and the present data on lobsters confirm the generalization that decapod crustaceans are less aggressive after exposure to the group housing situation. This same generalization has been demonstrated with various birds and mammals (Banerjee 1971; Kuo 1967), although it does not necessarily follow that the same mechanism is operating across various species.

Further research with the lobster will be necessary to determine the specific conditions responsible for the differences in aggressive behavior observed between lobsters housed communally and individually. It is reasonable to suspect that the previous history of agonistic behavior permitted by a group housing situation would play an important role in subsequent agonistic interactions (Scrivener MS 1971). It is also possible that chemical factors released in the high density holding conditions mediate the social interactions of the lobster. Atema and Engstrom (1971) reported, for example, that water from a tank that contained a recently molted female *Homarus* was sufficient to suppress the aggressive interactions between two animals in the hard shell stage of the intermolt cycle.

An understanding of the factors which control the agonistic interactions between lobsters in a communal housing situation would be of obvious value in the operation of holding pounds and other high population density aquaculture operations.

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Effect of Thermal Stress on Predator Avoidance in Sockeye Salmon

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SYLVESTER, J. R. 1972. Effect of thermal stress on predator avoidance in sockeye salmon. J. Fish. Res. Bd. Canada 29: 601–603.

Under laboratory conditions, predation rates of yearling coho salmon (*Oncorhynchus kisutch*) on sockeye salmon fry (*Oncorhynchus nerka*) increased with increasing acclimation temperature. Elevated temperature doses significantly decreased survival of sockeye salmon fry. The results suggest that under natural conditions, sudden increases in water temperature could alter predator–prey interactions of some fish by increasing predation mortalities.

SYLVESTER, J. R. 1972. Effect of thermal stress on predator avoidance in sockeye salmon. J. Fish. Res. Bd. Canada 29: 601–603.

Au laboratoire, le taux de prédation des saumons coho (*Oncorhynchus kisutch*) d'un an sur des alevins de saumons sockeye (*Oncorhynchus nerka*) augmente avec la température d'acclimatation. L'exposition à des températures élevées diminue sensiblement le taux de survie des alevins de saumons sockeye. Ces résultats donnent à entendre que dans la nature, des élévations subites de température peuvent affecter la relation prédateur–proie de certains poissons par un accroissement de la mortalité due à la prédation.

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THE demand for electricity is expected to double in the United States over the next 6–10 years, and it seems inevitable that the utilities will greatly expand the production of electric power. Along with this growth will be an increase in the quantity of coolant water needed by electric power plants (most new plants will be nuclear or fossil-fueled units that use water to condense steam discharged from turbines) and an increase in the quantity of heated coolant water (thermal discharge) that is put back into aquatic environments (Salo 1969).

Much of current research on thermal discharge is being conducted to show the effects of heating on aquatic environments in anticipation of the increased input (Adams 1969; Vernberg and Vernberg 1969). Under natural conditions, thermal plumes from electric power plants could have detrimental effects on the behavior of migrating salmonids. A vital question in regard to thermal pollution is: What effect will thermal discharge have on a prey's ability to avoid predation? The purpose of this work reported here has been to study the effect of moderate and severe thermal doses of short duration on the ability of sockeye salmon fry (*Oncorhynchus nerka*) to avoid predation by yearling coho salmon (*O. kisutch*) in laboratory aquaria.

Methods — Predators (28 yearling coho salmon) and prey (1000 sockeye salmon fry) were divided into three groups; each group was acclimated in holding tanks to water temperatures of 7, 12, or 17 C for at least 2 weeks before tests. These temperatures are within the natural environmental ranges of coho and sockeye salmon (Fry 1947, 1957; Brett et al. 1958). All fish were held under a constant photoperiod. Mean total lengths and weights

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of 24 predators and 120 prey chosen at random from the three acclimated groups were: coho 20.1 (range 17.7–23.1) cm; 68.8 (range 46.8–92.1)g; sockeye 3.2 (range 2.7–4.2) cm; 0.2 (range 0.1–0.5) g.

Tests were conducted in insulated tanks, 58 × 50 × 38 cm. Each tank contained approximately 84 liters of dechlorinated city water at acclimation temperature ± 0.5 C. Dissolved oxygen was maintained at 80–90% of air saturation values, and once through water flow in each tank was about 750–800 ml/min.

Eight prey and two predators acclimated to the same temperature were randomly selected from the holding tanks for each test. Predators were placed in test tanks 2–4 days before testing. All cover, such as heating units, chilling coils, and temperature probes, was removed before the prey were introduced to the tank containing predators. Prior measurements showed that the temperature remained stable in the insulated test tanks for more than an hour after heating units and chilling coils were removed.

Before tests were conducted, predators were held without food for 7 days at 7 C, 4 days at 12 C, and 3 days at 17 C on the assumption that digestion proceeds at a faster rate with increasing temperature. Brett and Higgs (1970) found that digestion rates increased with increases in temperature for fingerling sockeye salmon, and I am assuming that as digestion proceeds in coho salmon, the hunger drive increases. Prey were fed every second day except the day before tests.

A control series and two experimental series of tests were conducted at each acclimation temperature to study the effect of thermal doses of short duration on the prey. Tests in each series were replicated eight times. In the control series, the eight prey were first immersed in a temperature bath for 60 sec at acclimation temperature (7, 12, or 17 C), and then placed in the test tank at the same acclimation temperature with the two predators. In one experimental series, the eight prey were first immersed in a bath for 60 sec in water at acclimation temperature plus 10 C (17, 22, or 27 C); the prey were then placed in the test tank at acclimation temperature. In the other experimental series, the eight prey were first immersed for 5 sec in water at 30 C and then placed in the test tank at acclimation temperature. The predators received no immersion in elevated temperature baths, or thermal doses. Prior experimentation showed that the above immersion times and elevated temperatures were not lethal for sockeye salmon fry in the size range used here.

As each prey was eaten by the predators, a mark was made on an event recorder and the time in seconds was later determined from the tape.

Results and discussion — Mean total survival times of the prey in seconds for the control and experimental series at the three acclimation temperatures are given in Fig. 1.

The results of a factorial analysis of variance (Snedecor and Cochran 1967) with a square root transformation of the total survival times showed a significant decrease in total survival time with an increase in acclimation temperature ($P < 0.05$). The differences between prey survival times at acclimation temperatures and the survival times at elevated (dose) temperatures are highly significant ($P < 0.01$). There was also a highly significant interaction between acclimation temperature and the elevated dose temperatures ($P < 0.01$).

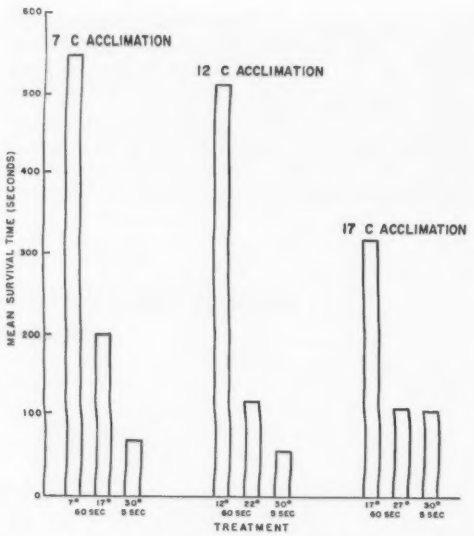

FIG. 1. Mean survival times of juvenile sockeye salmon fry exposed to predation after brief exposure to acclimation or elevated temperatures. (Each bar represents the mean of eight tests).

The results indicate that exposure of prey to elevated sublethal heat treatments for brief periods could markedly alter a predator–prey interaction by placing the prey at a relative disadvantage. The decrease in prey survival times at acclimation temperatures could have been due to an increase in predator forage activity, a decrease in the preys' swimming efficiency, or both. Because heat tolerance increases with increasing acclimation temperature (Brett 1944, 1952), the significant interaction between survival times at acclimation temperature and survival times at elevated temperatures could indicate increased thermal resistance in the sockeye salmon fry.

Although these results show that increases of 10 C above acclimation temperature and at 30 C are effective in decreasing sockeye fry survival in a simplified laboratory predation system, further experiments are needed to determine if increases of less than 10 C are effective in predator avoidance by sockeye salmon fry.

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The Relation Between Lobster Abundance, Sea Urchins, and Kelp Beds[1,2]

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MANN, K. H., AND P. A. BREEN. 1972. The relation between lobster abundance, sea urchins, and kelp beds. J. Fish. Res. Bd. Canada 29: 603–609.

When subtidal communities are disturbed and sea urchin populations expand, they frequently overgraze their food supply, eliminating large seaweeds from considerable areas. The hypothesis is advanced that the lobster is a key species, controlling sea urchin populations in eastern Canada, and that reduction of lobster populations below a critical density has led to overgrazing of seaweeds in many places.

MANN, K. H., AND P. A. BREEN. 1972. The relation between lobster abundance, sea urchins, and kelp beds. J. Fish. Res. Bd. Canada 29: 603–609.

Lorsque les communautés sub-cotidales sont dérangées et que les populations d'oursins se développent, celles-ci dénudent souvent, par excès de broutage, des étendues considérables de varechs, leur principale nourriture. Les auteurs émettent l'hypothèse que le homard joue un rôle-clef dans le contrôle des populations d'oursins de l'est du Canada, et que la diminution des populations de homards au-delà d'une densité critique a favorisé le broutage excessif des varechs en plusieurs endroits.

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WHEN one considers the management of a commercially important species in terms of its trophic system, the conclusions are often different from those obtained when considering only the population dynamics of the one species. Although the evidence is as yet incomplete, we draw attention to the possibility that heavy exploitation of lobsters may lead to the overgrazing of seaweed by urchins, with resultant loss of primary productivity.

[1]Contribution to the International Biological Programme CCIBP 128.
[2]Bedford Institute Contribution.

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Sea urchins and kelp — In St. Margaret's Bay, N.S., *Laminaria* spp. are the most important subtidal algae in terms of biomass (Mann 1972). However, within the *Laminaria* zone there are various-sized patches of almost bare rock that are characterized by high densities of sea urchins (*Strongylocentrotus droebachiensis*). The average biomass of sea urchins in bare patches is roughly 1200 g/m^2, while in kelp forests it is only 150 g/m^2 (Mann unpublished data). Himmelman (MS 1969) observed an inverse correlation between sea urchin and kelp abundance in Newfoundland, and other authors report similar observations with different sea urchin species (e.g. Jones and Kain 1967).

Higher densities of sea urchins outside the kelp beds might be explained in two ways. First, *S. droebachiensis* might show poor growth and survival in areas covered with kelp, and the bare patches would represent the preferred habitat. Alternatively, sea urchins might graze very actively on *Laminaria* and other species in the kelp forests, so that local high densities of sea urchins can eliminate nearly all the macroscopic algae from a patch.

The evidence appears to support the second explanation. Himmelman and Steele (1971) report that *S. droebachiensis* eats *Laminaria* readily in the laboratory, an observation confirmed by R. J. Miller and J. Field (personal communication). Further, Miller observed the recession of a *Laminaria* bed in St. Margaret's Bay by 3 m in one year when there was an abundance of sea urchins at the edge of it (Miller and Mann unpublished data). We have observed sea urchins within the *Laminaria* forest grazing on the blades and the stipes.

The second explanation is also consistent with studies carried out on other species of sea urchin. Recolonization of areas from which large macrophytes were absent has been shown to follow the removal of *S. purpuratus*, *S. franciscanus* (Paine and Vadas 1969), *Paracentrotus lividus* (Kitching and Ebling 1961), and *Echinus esculentus* (Kain and Jones 1966; Jones and Kain 1967). Cyclical interactions between *Strongylocentrotus spp.* and the giant kelp *Macrocystis* have been extensively documented (Leighton et al. 1966; North 1969; Pearse et al. 1970; Leighton 1971). Moreover, sewer outfalls appear to modify the interaction by providing nourishment that supports sea urchin populations in the absence of kelp, thus preventing kelp reestablishment (Pearse et al. 1970; Clark, 1969).

In Newfoundland, *S. droebachiensis* appears to control the distribution of *Laminaria* and *Alaria* (Himmelman MS 1969). Macrophytes there are most abundant where exposure to surf limits grazing by sea urchins, and only encrusting forms are found where high densities of sea urchins exist.

The control of sea urchin populations — These examples show that locally dense populations of sea urchins commonly overgraze their food supply. In areas where this does not occur, there must be some limitation on sea urchin population density other than food supply, and the most probable mechanism is predation. Paine and Vadas (1969) observed the starfish *Pycnopodia* reducing sea urchin density in local patches and suggested that this accounted for a patchwork of areas without sea urchins. In California, the sea otter (*Enhydra lutris nereis*) is a major predator of sea urchins. A local increase in otters was followed by a sharp decline in sea urchins and expansion of kelp beds (McLean 1962; North 1965). Thus, in California, sea otters may be indirectly responsible for the maintenance of kelp forests.

The role of lobsters — The prime candidate for the role of key predator on sea urchin populations in eastern Canada is the lobster. Lobsters in tanks in this laboratory readily eat sea urchins. Himmelman and Steele (1971) showed that two captive lobsters consumed 131 sea urchins, weighing a total of 342 g, in 7 months. At the peak period they were consuming 28 g per lobster per day. Rock crabs were also active predators but 2 crabs consumed only $\frac{1}{8}$ of the biomass consumed by the lobsters. Also, they were restricted to urchins of 38 mm or less, while lobsters attacked urchins up to 72 mm in diameter.

Miller et al. (1971) reported that in a study of food habits of lobsters near Prince Edward Island, sea urchin remains occurred in 28% of the stomachs examined. We have observed that, in the vicinity of lobster retreats in St. Margaret's Bay, sea urchins are less abundant than elsewhere, and broken sea urchin tests often occur.

Herring gulls prey on sea urchins in the intertidal zone, and several species of fish are predators in the sublittoral zone (Himmelman and Steele 1971), but the only predator that is subject to intense human exploitation, and hence might be expected to impart imbalance to the community, is the lobster. Reduction of lobster densities by fishing may be responsible for allowing sea urchin populations to reach densities high enough to clear away the kelp forest.

Anecdotal histories of several such sequences of events have been described to us by fishermen in St. Margaret's Bay. Intensive lobster fishing proceeded for several years in the same spot, after which sea urchins became abundant and kelp disappeared. This coincided with a period when lobster fishing was poor (probably because of overfishing), and the fishermen stopped fishing in the area until it returned to the normal situation: kelp forest, modest sea urchin abundance, and good lobster fishing. This normally took about 3 or 4 years.

If the foregoing ideas are correct, reduction in lobster population density below a certain critical level results not only in a decrease in the fishable

stock, but also in a population explosion of sea urchins, followed by overgrazing of the seaweeds that are the basic producers in the whole system. The large areas of relatively barren rock reported from many parts of the eastern coastline may, in one sense, be considered as man-made deserts.

Lobsters may then be considered as 'keystone' species, (Paine 1966, 1969), in that their predatory activities are a key factor in structuring the community.

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Synonymy of *Sebastes caenaematicus* with *Sebastes borealis*, and Range Extension Record

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WESTRHEIM, S. J., AND H. TSUYUKI. 1972. Synonymy of *Sebastes caenaematicus* with *Sebastes borealis*, and range extension record. J. Fish. Res. Bd. Canada 29: 606–607.

Sebastes caenaematicus Tsuyuki and Westrheim (1970) is synonymized with *Sebastes borealis* Barsukov (1970). Recorded geographical range of *S. borealis* has been extended southward in the eastern Pacific Ocean at least 600 miles, to Cape Flattery, Wash. (48°23′N lat), and probably 1000 miles, to Eureka, Calif. (40°46′N lat).

WESTRHEIM, S. J., AND H. TSUYUKI. 1972. Synonymy of *Sebastes caenaematicus* with *Sebastes borealis*, and range extension record. J. Fish. Res. Bd. Canada 29: 606–607.

Les auteurs synonymisent *Sebastes caenaematicus* Tsuyuki et Westrheim 1970 avec *Sebastes borealis* Barsukov 1970. Ils étendent l'aire connue de répartition géographique de *S. borealis* d'au moins 600 milles vers le sud dans le Pacifique oriental, jusqu'au cap Flattery, Washington (48°23′ latitude nord), et probablement de 1000 milles, jusqu'à Eureka, Californie (40°46′ latitude nord).

Received November 24, 1971

IN December 1970 we described a new rockfish species, *Sebastes caenaematicus* (Tsuyuki and Westrheim 1970). In the same year, V. V. Barsukov also described a new rockfish species, *Sebastes borealis* (Barsukov 1970). *S. borealis* had originally been recorded as *S. melanostomus* (Barsukov 1964), and we had noted that its published description closely resembled that of our *S. caenaematicus* (Tsuyuki and Westrheim 1970, p. 2249).

Recently, we have exchanged specimens of *S. borealis* and *S. caenaematicus* with Dr. Barsukov, and concur with him that based on physical morphology a single species is involved. By priority, the name of the new species is *S. borealis*. Volume 195 of Doklady contained Parts 4, 5, and 6, and we have assumed that Part 4 was published prior to December 30, 1970, the issue date of volume 27(12) of the Journal of the Fisheries Research Board of Canada.

V. V. Barsukov provided us with two specimens of *S. borealis* for examination. One specimen was deposited in the Museum of the Institute of Animal Resource Ecology (University of British Columbia, Vancouver, B.C.), catalog no. BC 71-26. The other specimen was deposited in the National Museum of Natural Sciences (Ottawa, Ont.), catalog no. NMC 71-579.

Two specimens of *S. caenaematicus* were sent to each of the following institutions, after publication of the description (catalog number if known, in parentheses):

Biological Laboratory
National Marine Fisheries Service
Auke Bay, Alaska, U.S.A. (AB 71–30)

British Museum of Natural History
London, England

California Academy of Sciences
San Francisco, Calif., U.S.A. (CAS-13462)

College of Fisheries
University of Washington
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Printed in Canada (J2349)

Scripps Institution of Oceanography
University of California, San Diego
La Jolla, Calif. 92037, U.S.A. (SIO 71-63)

United States National Museum
Washington, D.C., U.S.A. (USNM 205884)

Zoological Institute
Academy of Sciences
Leningrad, B-164, U.S.S.R. (MZIIL-40250)

Barsukov (1970) reported the range for *S. borealis* as 51°46′N lat, 158°38′E long (western Pacific Ocean) to 55°52′N lat, 135°21′W long (eastern Pacific Ocean). Tsuyuki and Westrheim (1970) listed the range for *S. caenaematicus* as 56°15′N lat (Cape Ommaney, Alaska) to 48°23′N lat (Cape Flattery, Wash.). A southward extension of the known range to Eureka, Calif. (40°46′N lat) is probable, based on reexamination of the physical morphology records of J. B. Phillips' specimen no. 617 (D. J. Miller personal communication). Unfortunately, the specimen could not be located.

Acknowledgments—The authors are indebted to W. E. Ricker (Nanaimo Biological Station) for providing a preliminary translation of Barsukov's description of *S. borealis*.

BARSUKOV, V. V. 1964. Key io the fishes of the family Scorpaenidae. *In* Soviet fisheries investigations in the northeast Pacific 53 (3): 226–262. Transl. from Russian by Israel Pogram for Sci. Transl., Jerusalem, 1968)

1970. Species composition of the genus *Sebastes* in the northern part of the Pacific Ocean. With description of a new species. Dokl. Akad. Nauk SSSR 195(4): 994–997.

TSUYUKI, H., AND S. J. WESTRHEIM. 1970. Analyses of the *Sebastes aleutianus-S. melanostomus* complex, and description of a new scorpaenid species, *Sebastes caenaematicus*, in the Northeast Pacific Ocean. J. Fish. Res. Bd. Canada 27: 2233–2254.

Recent Articles on FRB Investigations Published in Other Periodicals

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles, which henceforth may be obtained in reprint form only from the author or originating FRB establishment. The number following each title refers to the FRB establishment listed below.

(1) Fisheries Research Board of Canada
Biological Station
P.O. Drawer 100
Nanaimo, British Columbia

(2) Fisheries Research Board of Canada
Vancouver Laboratory
6640 N.W. Marine Drive
Vancouver 8, British Columbia

(3) Fisheries Research Board of Canada
Pacific Environment Institute
4160 Marine Drive
West Vancouver, British Columbia

(4) Fisheries Research Board of Canada
Freshwater Institute
501 University Crescent
Winnipeg 19, Manitoba

(5) Fisheries Research Board of Canada
Arctic Biological Station
P.O. Box 400
Ste. Anne de Bellevue, Quebec

(6) Fisheries Research Board of Canada
Biological Station
St. Andrews, New Brunswick

(7) Fisheries Research Board of Canada
Marine Ecology Laboratory
Bedford Institute
P.O. Box 1006
Dartmouth, Nova Scotia

(8) Fisheries Research Board of Canada
Halifax Laboratory
P.O. Box 429
Halifax, Nova Scotia

(9) Fisheries Research Board of Canada
Biological Station
St. John's, Newfoundland

1633. Zitko, V., and P. M. K. Choi. 1972. PCB and *p,p'*-DDE in eggs of cormorants, gulls, and ducks from the Bay of Fundy, Canada. Bull. Environ. Contam. Toxicol. 7: 63–64. (6)

1634. Wildish, D. J. 1971. Adaptive significance of a biased sex ratio in *Orchestia*. Nature 233: 54–55. (6)

1635. Evelyn, T. P. T. 1971. The agglutinin response in sockeye salmon vaccinated intraperitoneally with a heat-killed preparation of the bacterium responsible for salmonid kidney disease. J. Wildl. Dis. 7: 328–335. (1)

1636. Brett, J. R. 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Amer. Zool. 11: 99–113. (1)

Additional FRB Publications

The Fisheries Research Board of Canada also publishes a series of *Bulletins*, each on a specific topic. These are for sale by Information Canada, Ottawa, and remittances must be in advance, payable in Canadian funds to the order of the Receiver General of Canada. *Bulletins* are also available from local booksellers and Information Canada bookshops throughout Canada.

The *Annual Report* of the Board and the biennial *Review* of investigations are available free, on request. All publications may be referred to at Board establishments located at: Ottawa; Nanaimo and Vancouver, B.C.; Winnipeg, Man.; Ste. Anne de Bellevue, Que.; St. Andrews, N.B.; Halifax and Dartmouth, N.S.; and St. John's, Nfld

L'Office des recherches sur les pêcheries du Canada publie également une série de *Bulletins*, chacun traitant sur un sujet spécifique. Les publications de l'ORP sont vendues par Information Canada à Ottawa. Les remises, payables d'avance en monnaie canadienne, doivent être établies à l'ordre du Receveur général du Canada. Les *Bulletins* sont aussi en vente chez votre libraire et dans les librairies d'Information Canada.

Vous pouvez obtenir le Rapport Annuel et la Revue biennale gratuitement. On peut consulter ces ouvrages aux établissements de l'Office situés à Ottawa (Ont.), à Nanaïmo et à Vancouver (C.-B.), à Winnipeg (Man.), à Ste-Anne-de-Bellevue (P.Q.), à St-Andrews (N.-B.), à Halifax et à Dartmouth (N.-E.), et à St-Jean (T.-N.).

Journal
Fisheries
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Guide to Authors

Details on typing and other items in preparing copy are given in a guide for typists. Also, a list of recommended spellings of about 100 words common in fisheries journals is available from the Office of the Editor.

Editorial Practices

Abstracts should be provided in both English and French.

The *Style Manual for Biological Journals* (2nd ed. American Institute of Biological Sciences, 2000 P St. NW., Washington, D.C.) is, with few exceptions, used as the authority in matters of form. *Webster's Third New International Dictionary* is the standard for spelling and division of words in English; *le Grand Larousse Encyclopédique*, for those in French. Exceptions are made for manuscripts that follow the *Oxford English Dictionary* entirely. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. Manuscript reports are included in the list of references, but are identified both there and in the text by the letters "MS" before the year. The *Journal* follows the spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Third Edition, 1970), Special Publication No. 6 of the American Fisheries Society.

Notes are distinguished from *papers* on the basis of scope or completeness, rather than quality, of the research. They may be on problems with narrow, readily defined limits; on fishing gear or methods, or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued before completion; or on preliminary findings that warrant publication before problems are resolved satisfactorily. Or they may be used to establish priority in publication. They may be organized with as much flexibility as papers except that they may have no centered headings. They should take no more than four pages in the *Journal*.

In general, *series titles* should be avoided.

Illustrations

Line drawings are preferably made with black india ink on white drawing or tracing paper or on coordinate paper with blue grids. All lines, symbols, letters, and numerals must be neat, and legible when the illustration is reduced to the appropriate size. Drawings should be grouped, when feasible, for economy of space. Originals must be submitted and should be less than 20 inches in the greater dimension for full-page illustrations, and proportionately smaller for those taking less than a page. Drawings must not be rolled for mailing.

Prints of photographs should be made on glossy paper with a wide range in tone. They should be cropped, squared, and mounted with rubber cement on white cardboard, with no space between those arranged in groups.

Proofs and Reprints

Galley proof is sent to the author, and he is responsible for detecting errors in printing as well as in content.

Fifty reprints, without covers, are supplied free. Additional copies needed must be ordered, on the form provided, when the galley proof is returned.

Checklist on Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors. The same questions are recommended to referees who review manuscripts for the *Journal*.

General

Is there new knowledge in the report worth publishing?

Are the findings, interpretations, and conclusions sound, and relevant to the purpose of the study?

If the manuscript is merely confirmatory, is it worth publishing?

Does the manuscript need to be rewritten before the work can be assessed?

Is the contribution placed in the proper perspective concerning the state of knowledge of the subject?

Is the manuscript too long?

Are all the tables and figures needed, and organized for economy of space?

Would any of the text be clearer if condensed?

Should some of the data be made available separately, in a manuscript report or at a data repository?

Should the manuscript be condensed as a Note?

Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Are summary statements given at the beginnings of sections and paragraphs, and are details in sections and paragraphs relevant to their topics?

Are there inconsistencies between tables or figures and the text, or within the text?

If the manuscript is from a thesis, does it retain characteristics common in these but not desirable in journals?

Parts of the Manuscript

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Has the *introduction* all the important guideposts for orienting the reader?

Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data obtained?

Are generalizations on the *results* adequate?

Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

If there are loopholes in interpretation, are they acknowledged? Should they be overcome?

Should other interpretations be recognized?

Journal Fisheries Research Board Canada

Guide des auteurs

Des détails sur le tapage et certains autres item sont donnés dans le "Guide pour les secrétaires d'auteurs." Aussi, une liste d'épellations recommandées d'environ 100 mots relatifs aux articles sur les pêcheries est disponible au bureau du Directeur de la publication.

Disposition générale

Les résumés doivent être fournis en anglais et en français.

Le *Style Manual for Biological Journals* (deuxième édition, publié par l'American Institute of Biological Sciences, 2000, rue *P* N.-O., Washington, D.C.), a été adopté comme guide des auteurs. Le *Third New International Dictionary* de Webster, dans le cas de l'anglais, et le *Grand Larousse Encyclopédique*, dans le cas du français, font respectivement autorité pour l'orthographe et la séparation des mots. Une exception est faite à l'égard des travaux en anglais qui se conforment entièrement à l'*Oxford English Dictionary*. Les titres de périodiques sont abrégés selon la *Biological Abstracts*. Toute référence à la littérature doit suivre le système nom-année. Les rapports manuscrits sont inclus dans la liste des références, les lettres "MS" avant l'année les identifient dans les références et dans le texte. Le *Journal* se sert des épellations recommandées dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No 6 de l'American Fisheries Society.

Les *notes* se distinguent des écrits d'après l'étendue de la recherche plutôt que par la qualité de la recherche. Les notes peuvent être sur des travaux de recherche de portée restreinte, susceptibles de découler d'investigations plus considérables, pour la description de techniques de recherche et de méthodes de pêche, pour l'établissement de priorités de publication, et pour faire connaître les renseignements utiles tirés d'entreprises qui ont été interrompues avant d'avoir été achevées. Si la portée de la Note le permet, elle peut être disposée comme un mémoire. D'autre part, la disposition est flexible. La longueur ne doit pas dépasser quatre pages imprimées.

En général, les mémoires en série doivent être évités.

Les illustrations

Les dessins au trait doivent être exécutés à l'encre de chine sur papier à dessin blanc ou sur papier à calquer, ou sur papier à coordonnées avec quadrillage bleu. Les lignes, les symboles, les lettres et les chiffres doivent tous être propres. Ils doivent être lisibles quand ils sont réduits à la grandeur voulue pour la reproduction désirée. Les dessins doivent être groupés, si la chose est possible, de façon à utiliser tout l'espace disponible. Les originaux doivent être soumis et devraient mesurer moins de 20 pouces dans le sens le plus long pour les illustrations de pages entières, et proportionnellement plus petit pour les illustrations de moins d'une page. Les dessins doivent être postés à plat.

Les épreuves des photographies doivent être tirées sur papier glacé et accuser une gamme étendue de teintes. Elles doivent être coupées, dressées et montées, au moyen de dissolution, sur carton blanc, sans laisser d'espace entre celles qui sont disposées par groupes.

Epreuves et tires a part

Les épreuves en placards sont adressées à l'auteur et la responsabilité de toute erreur qui peut y rester lui incombe.

Cinquante tirés à part, sans couverture, sont fournis gratuitement. L'auteur peut profiter du renvoi des épreuves en placards pour commander d'autres tirés à part.

Liste de contrôles pour manuscrits

Une attention particulière portée sur les questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs. Les mêmes questions sont recommandées aux arbitres qui font la critique des livres pour le *Journal*.

Generalites

Est-ce que les connaissances nouvelles du rapport méritent d'être publiées?

Les découvertes, les interprétations et les conclusions sont-elles solides et pertinentes au but de l'étude?

Si le manuscrit est tout simplement corroboratif, mérite-t-il d'être publié?

Le manuscrit doit-il être récrit avant d'évaluer le travail?

La contribution est-elle placée dans une perspective appropriée relative à l'état des connaissances du sujet?

Le manuscrit est-il trop long?

Les tables et figures sont-elles toutes nécessaires et arrangées pour économiser le plus d'espace?

Le texte serait-il plus clair s'il était condensé?

Est-ce qu'une partie des données devrait être disponible séparément, soit dans un rapport ou dans un dépôt des données?

Le manuscrit devrait-il être condensé en une note?

Est-ce que la préparation du manuscrit suit la logique mentionnée dans l'introduction?

Y a-t-il des exposés sommaires au début de chaque section et paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents aux sujets?

Y a-t-il des contradictions entre les tableaux et les figures du texte, ou dans le texte même?

Si le manuscrit est tiré d'une thèse, contient-il des caractéristiques communes à cette dernière, mais indésirables dans un journal?

PARTIES DU MANUSCRIT

Le titre renferme-t-il le contenu du rapport?

Le résumé donne-t-il l'essentiel des connaissances nouvelles?

L'introduction a-t-elle tous les points importants afin d'orienter le lecteur?

Le renvoi bibliographique se limite-t-il à la définition du problème?

Les détails du matériel et des méthodes employées sont-ils limités à un minimum pour que les scientifiques comprennent le but de l'étude et puissent porter un jugement adéquat sur les données obtenues.

Les généralisations sur les résultats sont-elles adéquates?

Les conclusions sont-elles déduites des résultats?

La discussion est-elle limitée à l'interprétation et la signification de ces découvertes?

S'il y a des échappatoires dans l'interprétation, sont-elles reconnues? Devraient-elles être maîtrisées?

Devrait-on accepter d'autres interprétations?

Journal
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Board
Canada

Guide for Typists Preparing Copy

Read the "Guide to Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 8.5 × 11 inches (21.5 × 28 cm). If possible, use paper with the lines numbered in the margin. Leave all margins at least 1 inch (2.5 cm) wide. Use a nylon or carbon ribbon and keep the typewriter keys clean.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize only the first word and proper names and adjectives. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numbers. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (Appendix A). Type the abstract on a separate page (Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send two copies (the ribbon copy and a carbon copy or a photocopy) to the Office of the Editor.

Tables

Examine the current volume of the *Journal* to see how tables are set up (Appendix C).

Note especially the following concerning *numbered tables*:

Type each table on a separate page, using paper without the lines numbered.

Number the tables with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, they are typed with the text, they seldom need horizontal lines, and the data are arranged in as few rows as possible (Appendix C).

Illustrations

Send the original and two clear copies of each illustration with the manuscript. At the lower left of each figure and copy, give the author's name and the figure number. Also type each caption with its figure for identification. For photographs, type this information on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas

Leave three spaces above and below lines that have much material in superscripts or subscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter l and the numeral one, and between the capital letter O and the numeral zero. Make other explanatory notes similarly.

References

Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style that is used in the *Journal* (Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list, but if an abbreviation is in doubt, type the name in full.

Spellings

A list of about 100 words common in fisheries journals is given in Appendix F.

Appendices

Appendices A to F are available on request from the Office of the Editor.

Journal Fisheries Research Board Canada

Guide pour les secrétaires d'auteurs

Lisez le "Guide des auteurs" dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de taper ou d'arranger les détails, suivez la pratique du *Journal*.

Tapez le manuscrit sur un papier blanc et non un papier pelure, mesurant de préférence 8½ × 11 po. (21.5 × 28 cm) et laissant une marge d'au moins 1 po. (2.5 cm). Si possible, employez un papier avec des lignes numérotées dans la marge. Employez un ruban nylon ou carbone et gardez les clés du dactylo nettes.

Chaque partie du manuscrit doit être tapée à double-interligne au moins. La chose est particulièrement importante dans le cas des tableaux, légendes d'illustrations, renvois au bas de la page et listes de références bibliographiques. Evitez de souligner à moins que la matière ne soit en italique. Mettez en retrait la première ligne de chaque paragraphe du texte, ainsi que de chaque légende et renvoi.

Dans les titres et en-têtes, n'employez la majuscule que pour le premier mot, les noms propres et les adjectifs. Pour les petites majuscules, utilisez les petites lettres.

Indiquez tous les renvois au texte par des chiffres arabes en-tête. Numérotez-les consécutivement à travers le texte en commençant par ceux de la page-titre. Placez chaque renvoi immédiatement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit donner que le titre du sujet, le nom et l'affiliation de l'auteur ou des auteurs, et tout autre renvoi utile (Appendice A). Tapez le résumé sur une page séparée (Appendice B). Numérotez chaque page, débutant avec la page-titre.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et un double du travail au Directeur de la publication.

Tableaux

Consultez une copie du *Journal* pour savoir composer les tableaux et placer les lignes qui y entrent (Appendice C).

Portez une attention particulière à ce qui suit concernant les *tableaux numérotés*.

Tapez les tableaux sur des pages séparées, en utilisant du papier sans lignes numérotées.

Numérotez les tableaux avec des chiffres arabes.

Employez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, et très rarement ailleurs. N'employez jamais de lignes verticales; de préférence, laissez de l'espace supplémentaire.

Indiquez les renvois dans les tableaux au moyen de petites lettres italiques en position supérieure et tapez-les au bas de la page.

Placez les tableaux après la liste de références.

A l'endroit où un tableau est mentionné pour la première fois, tapez dans la marge "Tableau (- - -) près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, ils sont tapés avec le texte. Ils ont rarement besoin de lignes horizontales, et l'information est préparée de façons à prendre le moins de rangées possibles.

Illustrations

Joignez au manuscrit expédié le dessin original des illustrations et des photocopies en deux exemplaires.

Au bas et à gauche de chaque figure et photocopie, inscrivez le nom de l'auteur et le numéro de la figure. Aussi, tapez chaque légende avec sa figure pour fin d'identification. Pour les photographies, tapez l'information sur une lisière de papier et collez-la au dos de la photographie. N'écrivez pas et ne tapez pas sur la photographie même. Tapez ensemble sur une feuille séparée et par ordre consécutif les légendes des illustrations, et intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, tapez dans la marge "Fig. (- - -) près d'ici."

Equations, formules et expressions mathematiques

Laissez trois espaces au-dessus et au-dessous des lignes qui contiennent du matériel en positions supérieures ou en positions inférieures, et au-dessus et au-dessous d'équations et de formules. Dans les différentes expressions, placez chaque composante dans sa position appropriée (Appendice D).

Indiquez les symboles clairement. Dans la marge, épelez les lettres grecques la première fois qu'elles apparaissent et faites une distinction entre la lettre "l" et le chiffre "un" et entre la majuscule "O" et le

chiffre "zéro." Procédez de la même façon pour d'autres notes explicatives.

References

Vérifiez le texte afin d'assurer que sont mentionnées toutes les références ou renvois de la liste. Tapez, à doubles interlignes et de la façon prévue (Appendice E) pour le *Journal*, la liste de références. Les noms de journaux sont abrégés suivant la *Biological Abstracts*, mais s'il y a doute, écrivez le nom au long.

Vocabulaire

Une liste d'environ cent mots relatifs aux articles sur les pêcheries est disponible au bureau du Directeur de la publication (Appendice F).

Appendices

Les appendices de A à F sont disponibles sur demande au bureau du Directeur de la publication.

Seminar

Toward a Unified Concept of Biological Waste Treatment Design

October 5–6, 1972

This seminar will be sponsored by the International Association on Water Pollution Research and will be held at the Georgia Institute of Technology, Atlanta, Georgia. This conference is designed to demonstrate a unified approach to biological waste treatment design. Mathematical models in present use will be discussed and evaluated by experts from all parts of the world. Factors affecting use of models and their applications will be presented.

REGISTRATION FEE: $125.00

Further information may be obtained by contacting:

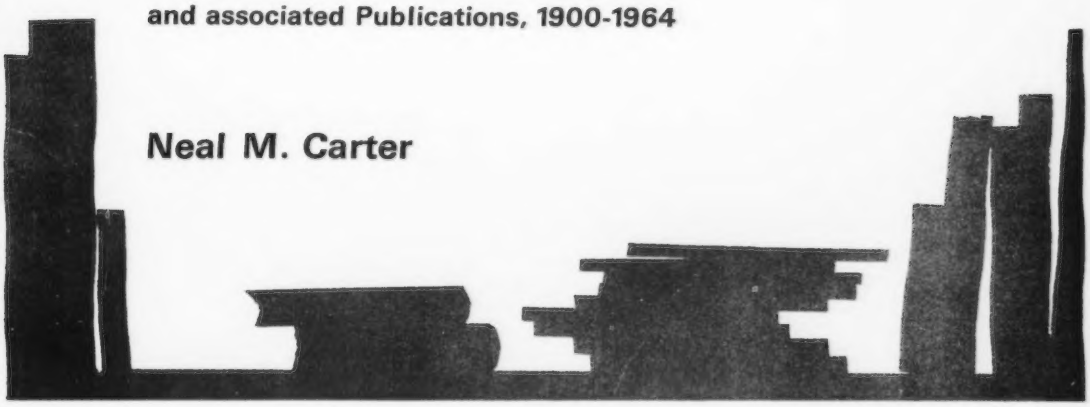
Professor Fred G. Pohland
Civil Engineering Department
Georgia Institute of Technology
Atlanta, Georgia

Bulletin 164

Index and List of Titles,

Fisheries Research Board of Canada and associated Publications, 1900-1964

Neal M. Carter



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Vancouver: *657 Granville Street*

Subsequent annual Indexes and Lists of Publications (1965–1971) may be obtained free from:

Office of the Editor
Fisheries Research Board of Canada
Department of the Environment
116 Lisgar Street
Ottawa, Ontario K1A 0H3

Journal of the Fisheries Research Board of Canada

Volume 29, No. 5, May 1972

JFRBCA29(5)469-609(1972)

An evaluation of two tags with northern pike (*Esox lucius*) **G. D. Koshinsky** 469–476

Population biology of alewives, *Alosa pseudoharengus*, in Lake Michigan, 1949–70 **E. H. Brown Jr.** 477–500

Tissue culture bioassay method for water pollution with special reference to mercuric chloride **M. F. Li and G. S. Traxler** 501–505

Distribution of herring (*Clupea harengus*) larvae along the southern coast of Nova Scotia with observations on their growth and condition factor **D. D. Sameoto** 507–515

Croissance en longueur et en poids des perchaudes *Perca flavescens* de la Grande Anse de l'île Perrot au lac Saint-Louis **R. Fortin et E. Magnin** 517–523

Effects of dressing and cooking on DDT concentrations in certain fish from Lake Michigan **R. E. Reinert, D. Stewart, and H. L. Seagran** 525–529

Morphology and enzyme histochemistry in the liver of largemouth bass (*Micropterus salmoides*) **D. E. Hinton, R. L. Snipes, and M. W. Kendall** 531–534

The American eel (*Anguilla rostrata*) in eastern Lake Ontario **D. A. Hurley** 535–543

Postglacial dispersal of four deepwater fishes on the basis of new distribution records in eastern Ontario and western Quebec **M. J. Dadswell** 545–553

An experimental study of feeding behavior and interaction of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*) **D. C. Schutz and T. G. Northcote** 555–565

The bacterial population in vertical flow tray hatcheries during incubation of salmonid eggs **T. J. Trust** 567–571

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Growth of larval herring (*Clupea harengus*) in the Bay of Fundy and Gulf of Maine area **N. Das** 573–575

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